Feeding ecology of Yakusima macaques (Macaca Fuscata yakui) in warm-temperate forest of Yakushima island, Japan(Dissertation_全文)

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主論文の要旨

屋久島照葉樹林内のヤクシマザルの遊動　採食行動を環境要因から検討した。

ヤクシマザルは主に果実・葉　種子　花および昆虫等を採食していたが、食物の季節的変動は非常に大きかった。各食物品目の森林内の現存量および気温と各食物の採食時間の関係を分析した結果、彼らの食物選択には食物現存量だけでなく気温も大きな影響を及ぼしていることが判明した。気温が体温維持のエネルギー消費量とタンパク質源である昆虫等の採食可能性を変化させることによりサルの食物選択に影響を与えたものと考えられた。

ヤクシマザルの１日当たりの移動時間と採食時間は食物によって大きく変化していた。彼らは単位重当たりの熱量は高いが現存量の少ない果実などを採食する場合には、移動時間を長く採食時間を短くしていた。一方、熱量は低いが発見しやすい葉などを採食する場合には逆の傾向を示した。基本的に彼らは食物の発見に関わる出費と、採食した場合の利益をバランスさせる戦略をとっていたと考えられた。そして、これら食物、採食　移動時間などは食物環境の変動により、短期間に複雑に変化することも示された。

ヤクシマザルの遊動域は食物の分布状態に対応していた。彼らが果実を主に採食していた時期では果実量の高い地域を集中的に利用していた。ところが、彼らが葉も頻繁に採食していた時期では、必ずしも葉量の高い場所を遊動せず、多種類の葉を利用できる場所を利用していた。彼らは多種類の葉を採食することで単一の二次代謝物の蓄積を避け、消化効率を上げていたことが示唆された。

最後に、群れ内の個体同士の活動の同調性が、群れサイズおよび利用する食物により、いかに変化するかを検討した。大きな群れ（15-19頭）と小さな群れ（5-8頭）における個体間の活動の同調性を調べた結果、いずれの群れでも個体間で活動を同調させる傾向がみられた。しかしながら、大きな群れでは小さな群れに比べ、食物必要量が多い、群れ内の採食競合が強い、群れを見失いにくいなどの理由から、同調の程度が低いことが示唆された。

主論文

Feeding ecology of Yakushima macaques (*Macaca fuscata yakui*) in warm-temperate forest of Yakushima island, Japan

（照葉樹林に生息するヤクシマザルの採食生態）

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主論文

THESIS

Feeding ecology of Yakushima macaques (*Macaca fuscata yakui*) in warm-temperate forest of Yakushima island, Japan

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CONTENTS

ABSTRACT

Feeding ecology of Yakushima macaques (*Macaca fuscata yakui*) in warm-temperate broad-leaved forest of Yakushima island was examined in relation to environmental factors.

Yakushima macaques fed mainly on fruits, seeds, leaves, flowers and insects. However, seasonal variation in their diet was great. Dietary selection by monkeys was examined in relation to food availability and air temperature. Multiple regression analysis indicated that both food availability and temperature influenced the selection of foods. Feeding on young leaves, seeds and flowers were affected more by availability, whereas feeding on fruits, mature leaves and fallen seeds were affected more by temperature. Feeding on insects was strongly correlated with temperature, though their availability was not assessed. It is suggested that temperature influences dietary selection of Yakushima macaques by changing the energy expenditure required for thermoregulation, and through its influence on the availability of insects, which are an important protein source for the monkeys (Chapter 1).

The activity budget and diet of Yakushima macaques were investigated. Both time spent feeding and moving varied considerably between half-months. However, total time spent in active behaviors (feeding time plus moving time) was stable. Time spent feeding on mature leaves, young leaves, flowers or fallen seeds was positively correlated with total time spent feeding, and was negatively correlated with time spent moving. By contrast, time spent feeding on fruits, seeds, insects or fungi showed opposite trends with feeding time and moving time. If time spent feeding on fruits, which provide more energy and may require less manipulation than other foods, is regarded as a benefit, and moving time as a cost, Yakushima macaques seemed to employ a strategy that balanced the costs and benefits of foraging (Chapter 2).

Rapid changes in the foraging patterns of Yakushima macaques are described. These occurred from May to June and were apparently associated with changes in the

availability of *Myrica rubra* fruit. Before the ripening of the fruit the monkeys moved slowly and spent much time feeding on the leaves and buds of many species. In this period, they ranged mainly in an area with a high leaf-food species diversity. When *M. rubra* fruit began to ripen, the monkeys fed intensively on them, though their activity budget did not change. They shifted their range to an area where *M. rubra* trees were densely distributed. As the total number of the fruit decreased, the monkeys gradually shifted to feed on insects and other fruits, and spent more time moving, moved at higher speeds and ranged more evenly. In terms of moving cost and diet quality, monkeys shifted their foraging pattern according to the availability of *M. rubra* fruit from a "low-cost, low-yield" strategy to a "low-cost, high-yield" strategy, and then to a more costly strategy. The ability to make such rapid shifts in foraging pattern may allow Yakushima macaques to make effective use of the highly variable food supply within their small ranging area (Chapter 3).

Synchrony of behavior among individuals in a group of Yakushima macaques was examined in relation to group size and food resources. The degree of synchrony was greater when the group was small (5-8 individuals) than when it was large (15-19 individuals). Diet did not affect the degree of synchrony. However, the duration of the "active phase", in which most of members of the group synchronized feeding and moving, was shorter when they fed mostly on fruits (fruit-eating season) than when they fed mostly on other foods (non-fruit-eating season). When the group was large the monkeys ranged over a greater area and foraged in fewer trees during the fruit-eating season than during the non-fruit-eating season. However, this tendency was not so clear when the group was small. These results suggest that the extent to which the distribution of food resources determines patterns of foraging increases with group size, and that monkeys in larger groups must reduce levels of intra-group food competition in order to get sufficient food (Chapter 4).

Chapter 1

Dietary selection by Yakushima macaques: The influence of food availability and temperature

1.1 INTRODUCTION

For efficient intake of nutrients, animals should vary their selection of foods in relation to number of factors including food quality and availability in the habitat, and the animals' metabolic rate (Schoener, 1971). The relationship between selection of plant foods, such as fruits, flowers, leaves, and their availability has recently been studied in several primate species (e.g. Estrada, 1984; Harrison, 1984; Yeager, 1989; Davies, 1991; Lucas and Corlett, 1991; Stanford, 1991; Strier, 1991; Newton, 1992). These studies suggested that for some foods feeding is related to availability, while for others it is not. Foods which have relatively high quality, and which vary greatly in availability, such as fruits, flowers, and young leaves, tend to be fed on according to their availability (e.g. Estrada, 1984; Harrison, 1984; Yeager, 1989; Lucas and Corlett, 1991; Newton, 1992).

Selection of foods by primates is also related to body weight (Clutton-Brock and Harvey 1977; Sailer *et al.,* 1985), age and sex (Gautier-Hion, 1980; Harrison, 1983, Watanuki and Nakayama, 1993). These factors influence the nutritional requirements of the individual animals. Larger species tend to feed more on leaves because they need more energy, but have a lower metabolic rate per body weight than smaller species (Sailer *et al.,* 1985). It has also been suggested that female monkeys tend to feed more on foliage than males in some species, because of a greater protein requirement (Gautier-Hion 1980; Harrison, 1983), and pregnancy and lactation may lead to an increase in female metabolic rate (Portman, 1970). In addition, the type of digestive system a species has, i.e. monogastric or ruminant, will be related to selection of fibrous foods, reflecting the animal's ability to break down plant fibers (Davies, 1991).

Air temperature influences the metabolic rate of monkeys by causing changes in the energy required for thermoregulation. Air temperature might therefore be expected to be one of the factors influencing dietary selection. Patas monkeys increase

their metabolism below around 20° C (Mahoney, 1980), night monkeys do so below around 35° C (Le Maho *et al.*, 1981), slender lorises below around 35° C (Muller *et al.*, 1985) and Japanese monkeys below around 30° C (Nakayama *et al.*, 1971). Heat produced by a female Japanese monkey of 8 kg is 515 W/day at 30° C and 1262 W/day at 5° C (Nakayama *et al.*, 1971). The former figure will be almost equal to the basal metabolic rate. Therefore, as temperature decreases, energy requirements increase (cf. Iwamoto and Dunbar, 1983), and it is predicted that monkeys will adjust their selection of foods to increase the efficiency of nutritional intake. However, the influence of temperature on the selection of foods by primates has received only little attention (however, see Watanuki and Nakayama, 1993).

The purpose of this paper is to examine the influence of air temperature on dietary selection. Yakushima macaques (*Macaca fuscata yakui*), the subject of this paper, are one of two subspecies of Japanese macaques (*M. fuscata*) and are found only on Yakushima island. They inhabit forest dominated by evergreen broad-leaved trees, where temperature varies from 5 to 31° C over a year. The monkeys feed mainly on fruits, seeds, leaves and insects (Maruhashi, 1980). Seasonal variation of diet is great, though details of their diet have been reported only for limited months (August to December: Maruhashi, 1980; May and August: Maruhashi, 1986). Thus, Yakushima macaques are a good subject for testing influences of food availability and temperature on dietary selection. This paper firstly describes characteristics of the food availability at different times of year and patterns of consumption from 10 months' data. Next, the influence of food availability and temperature on dietary selection are examined.

1.2 STUDY AREA

The study was carried out on the northwest coast of Yakushima island (N 30°,

E 131°), Japan. Annual rainfall is about 2600 mm (Tagawa, 1980). Mean monthly maximum temperature varied from 13 (January) to 28° C (August) throughout study period. The area is covered by primary and secondary warm temperate broad-leaved forest (0-350 m above sea level). The forest consists mainly of evergreen species of Fagaceae, Myrsinaceae and Lauraceae. Deciduous species including several *Ficus* species also exist. The study area contains various types of vegetation: primary forest, mixed primary and secondary forest, patches of early successional deciduous trees along the road, and coastal vegetation. The diversity of plant species which compose the forest is high (Tagawa, 1980).

1.3 METHODS

Feeding behaviors

Feeding behaviors of Yakushima macaques in a well habituated group (P Group: Hill, 1991a) were observed intermittently from January 1990 to April 1992. The group size varied from 5 to 19 members (2 to 6 adult males, 2 to 5 adult females) as a result of births, deaths and migration by males.

Every 10 minutes a 5-minute scan (Altmann, 1974) was made during which the behavior of all visible members of the group, excluding suckling infants, was recorded. Food items, i.e. parts and species of woody plants, herbs, ferns, fungi, insects and other items monkeys fed on, were also recorded.

Food items eaten by monkeys were classified into 7 categories according to their spatial distribution and nutritional characteristics, as follows. Fruits: whole fruits including seeds. Seeds: seeds and nuts on trees without pulp. Fallen seeds: fallen nuts, seeds and dried fruits in the leaf litter on the forest floor. Flowers: nectar and petals. Mature leaves: leaves completely spread out. Young leaves: immature leaves, buds and new shoots. Insects: insects and other animal matter. Time spent feeding on each

item was determined by calculating the number of records of feeding on that food item as a proportion of the total number of feeding records in each month, regardless of sampling year. Annual time spent feeding on each item was calculated by averaging values of time spent feeding on the item of each month.

Food items which account for 1 % or more of time spent feeding over 10 calendar months were regarded as "main food items" and those which account for 0.1 % or more were regarded as "common food items"

Measuring of temperature

A maximum and minimum thermometer was fixed to a tree in the forest at 1.3 m above the ground, 7 m away from an ephemeral stream. On every day of field work, the maximum and minimum temperatures were recorded. Daily maximum temperatures were recorded 30 times on average (range 14-65 times) for each calendar month. The data were combined and averaged each month regardless of sampling year.

Survey of food availability

Vegetation of the study area was surveyed from September, 1990 to May, 1992. Ninety-eight 5m × 50m belt transects were established uniformly over 25 ha within the range of the study group (about 32 ha). The following method was used to estimate the crown area of all trees of 5cm or greater DBH which lay on the transect belt. First, a line was measured which corresponded to the crown width at its greatest point (A). Next, a second line (B) which was perpendicular to the first was measured. Then, the crown area was expressed as the area of an ellipse with long axis (A) and short axis (B). This method produces an estimate of actual crown area which can be compared between species at one location, and between locations (Agetsuma and Noma, in press). Estimated crown areas were summed for each species.

The period during which each plant food item was available was censused

during the observation of monkeys and vegetation survey. Calendar months when at least one individual of a species of food plant had fruits, seeds, flowers, mature leaves or young leaves available were recorded.

The availability of each category of plant foods (excluding fallen seeds) in each calendar month was calculated as follows. For each calendar month, the total crown area of common food species of that category, which were available in that month regardless of sampling year, was summed. The month with maximum total crown area was given a value of one, and total crown area in the other months was expressed as a proportion of this. This value is described as the index of availability.

Foraging on the ground for fallen seeds has been observed frequently in Yakushima macaques from winter to spring (Hill, 1991a). For estimating the availability of fallen seeds, five sites where the monkeys foraged on the ground were selected for sampling. The sampling was carried out 5 times over 8 months on 17 and 22 September, 9 November, 8 and 9 December in 1991, 3 and 4 February, 24 April in 1992. Each time, a 25 m^2 quadrat was set at each of five sites and fallen seeds within the quadrats were sampled. The sampled seeds were identified and counted in the laboratory.

Availability of fallen seeds was expressed as the density of fallen seeds of common foods. Then, the availability index of the item was expressed by the relative density of each sampling month.

1.4 RESULTS

A total of 10,733 feeding records were obtained during the study period. Feeding records in July and October were too few to be analyzed. Yakushima macaques fed on at least 84 species (151 items) of plants in the study period. Fruits, seeds and nuts of 58 species, flowers of 14 species, leaves, shoots and buds of 45

species of woody plants were eaten, in addition to herbs and grasses of 3 species, ferns of 4 species and several species of unidentified fungi. The monkeys also fed on several species of insects and vertebrates. There were 21 main food items (17 species) which accounted for 1 % or more of time spent feeding over 10 calendar months (Fig. 1.1) and 69 common food items (51 species) which accounted for 0.1 % or more (Table 1.1).

Available periods and consumption patterns for each food item

Monkeys fed on the seed of *Lithocarpus edulis* (Fagaceae) in the trees in August and September. After this, they started to forage intensively on fallen seed on the ground. The density (No./m^2) of seed on the ground varied from 3.26 (September), 8.04 (November), 5.18 (December) to 2.05 (February). By the last sampling time, in April, the density of seed was only 0.50, and 6.5% of them had already germinated. The estimated available period for the fallen seed was therefore considered to be from August to March.

Mature fruit of *Neolitsea aciculata* was available from September to November. Although there was one feeding record for immature fruit of this species in February, the available period was regarded to be from September to November.

Available periods and consumption patterns of 21 main food items are shown in Figure 1.1. Leaf-food items tended to be available for long periods, but were consumed in only small amounts each month. On the other hand, fruit-food items tended to be available for shorter periods and were consumed in much greater amounts during that time.

Characteristic plant food items of Yakushima macaques could be classified into 3 types, in terms of available periods and consumption patterns (Fig. 1.1 and Table 1.1). Type 1 foods were available for 6 months or more out of the 10 calendar months, though they were fed on in less than two thirds of the available period. Most

of the common mature leaf-food items were classified as Type 1.

Type 2 foods were available for 6 months or more and were fed on in more than two thirds of the available period. Three main mature leaf-food items, including *Oreocnide pedunculata* and *Trema orientalis*, which are pioneer species found along streams and roadsides, and 5 common fruit-food items including 2 species of *Ficus*, *O. pedunculata*, and the fallen seed of *L. edulis*, were classified as this type.

Type 3 foods were available for less than 6 months. Most of common fruit-food items, seed-food items and young leaf-food items, and all common flower-food items were classified as Type 3.

Time spent feeding on Type 1 foods was 15.4 %, that on Type 2 foods was 35.0 % and that on Type 3 foods was 29.6 % on average over 10 months'. Type 2 foods included only 7 items (Table 1.1), however this type constituted a considerable proportion of the diet of the monkeys.

Seasonal variation of diet

Time spent feeding on each food category in each month is shown in Figure 1.2. On average over the 10 months, 28.6% of feeding time was spent on fruits, 18.5 % on mature leaves, 18.1 % on fallen seeds, 10.9 % on seeds, 8.9 % on insects, 4.9 % on flowers and 3.9 % on young leaves. There were significant monthly differences in proportions of the 7 food categories in the diet (Chi-square > 8,000, $p<0.001$, df1=6, df2=9). Variation in the diet was greatest from December to May. During this period, the top category of food changed in turn from fruits (December), fallen seeds (January and February), flowers (March), mature leaves (April) to fruits (May). By contrast, from May to December, fruit feeding was dominant. Various species of insects were fed on throughout the year, but insect-eating was most common in the summer.

Influences of food availability and temperature on dietary selection

Availability of each plant food category and mean maximum temperature for each month are shown in Figure 1.2. Monkeys fed on fallen seeds intensively from September to March (Fig. 1.2). Only the seed of *L. edulis* reached the main and common food criterion within the food category of fallen seeds. Moreover, 88.5% of all sampled fallen seeds from 5 quadrats (N=2,625) were of this species. Monthly density of the seed varied greatly on forest floor as mentioned above. The availability index of this item was expressed as the relative density in each month; August: 0.21 (value of Sep. divided by 2), September: 0.41, November: 1.00, December: 0.64, January: 0.45 (mean values of Dec. and Feb.), February: 0.25, March: 0.16 (mean values of Feb. and Apr.), April: 0.06. The availability in other months were considered to be zero.

Correlations between availability of each food category and temperature are examined in Figure 1.2 (Table 1.2). The availability of both fruits ($r=-0.76$, $p<0.05$, $n=10$) and flowers ($r=-0.78$, $p<0.01$) were negatively correlated with temperature. The availability of other food categories had no significant correlations with temperature.

Table 1.3 shows correlations between feeding on each food category. Significant positive correlations were found between feeding on seeds and insects ($r=0.67$, $p<0.05$), and between mature leaves and young leaves ($r=0.76$, $p<0.01$). On the other hand, negative correlations were found between feeding on mature leaves, and fruits ($r=-0.72$, $p<0.05$), seeds ($r=-0.66$, $p<0.05$) and insects ($r=-0.59$, $p<0.1$), and between fallen seeds and insects ($r=-0.59$, $p<0.1$).

Coefficients of simple regressions between feeding on each food, and its availability and temperature are shown in Table 1.4. Feeding on young leaves ($r=0.75$, $p<0.05$), flowers ($r=0.62$, $p<0.1$) and seeds ($r=0.86$, $p<0.01$) were positively correlated with their availability. Feeding on seeds ($r=0.76$, $p<0.05$) and insects ($r=0.92$, $p<0.001$) showed positive correlations with temperature. On the other hand, mature

leaves ($r=-0.56$, $p<0.1$) and fallen seeds ($r=-0.82$, $p<0.01$) showed negative correlations with temperature.

The degree to which food availability and temperature influenced feeding on each plant food category was analyzed using multiple regression analysis. Multiple and partial regression coefficients for each food category are shown in Figure 1.3. Feeding on seeds ($R=0.95$, $p<0.001$) and fallen seeds ($R=0.82$, $p<0.05$) showed significant multiple regression coefficients. Partial regression coefficients indicated that temperature was more clearly related to feeding on fruits, mature leaves and fallen seeds, than was food availability. Higher temperature was associated with an increase in feeding on fruits, and a decrease in feeding on mature leaves and fallen seeds. This means that even if availability of these food categories remained unchanged, time spent feeding on these foods would change with temperature. On the other hand, availability was more strongly associated with feeding on young leaves and flowers.

1.5 DISCUSSION

Characteristics of food items

Food items (species and part) of Yakushima macaques may be classified into 3 types in terms of periods of availability and patterns of consumption (Table 1.1). Type 1 foods were available for a long period but were consumed for a limited period. Most mature leaf-food species were classified as Type 1. Type 2 foods were available and consumed over a long period. This type consisted mainly of several fruits and some mature leaves. Type 3 foods were available and consumed for short periods. Most young leaf-foods, seed-foods and fruit-foods and all flower-foods were classified as Type 3.

Fruits, seeds and flowers are regarded as high quality foods, predicting more readily available energy, and fewer secondary compounds than leaves (Harrison, 1985;

Milton, 1993). Therefore, Type 1 foods consisted mainly of lower quality items and Type 3 of higher quality items, in terms of energy. Type 2 foods consisted of a mixture of higher and lower quality items. Yakushima macaques fed basically on stable Type 2 foods, and opportunistically on variable Type 3 foods. Monkeys fed on Type 1 foods mainly when Type 2 and Type 3 foods were difficult to obtain, from March to May (Fig. 1.1).

Quality of unit weight of fallen seeds should be approximately equal to seeds on trees, in terms of readily available energy. However, searching for dispersed fallen seeds in the leaf litter may take longer time, but require less energy because the monkeys do not have to move on and climb up and down trees. Therefore, in total, feeding on fallen seeds will have yielded relatively low nutritional intake with low cost in a unit time.

Mature leaves are regarded as a low quality food in terms of readily available energy (Harrison, 1985; Chapman and Chapman, 1990; Milton, 1993). However, mature leaves were very important foods for the monkeys as "back stop" foods (Harrison, 1984). Mature leaves would insure against the failure of opportunistic foraging for higher quality, but more variable Type 3 foods by assuring reliable food intake. Green monkeys (Harrison, 1984) and capped langurs (Stanford, 1991) may also have similar "back stop" foods. However, to avoid the accumulation of secondary compounds, monkeys may have to feed on various species of mature leaves rather evenly in each month (Fig. 1.1)

Seasonal variation of diet

Yakushima macaques showed large seasonal variation of diet (Fig. 1.2). Their monthly diet varied from nearly folivorous, fruigivorous, to mixture of fruigivorous and insectivorous (Hill, 1991b). Great seasonal variation in diet has also been reported for other populations of Japanese macaques, both in cool temperate

(Suzuki, 1965; Koganezawa, 1975; Wada, 1980) and in warm temperate regions (Iwamoto, 1982). Thus, great variability of diet may be commonly found in any habitat of Japanese macaques.

Influence of temperature on dietary selection

The results of this study have shown that dietary selection by Yakushima macaques is influenced, not only by the existence of alternative foods and food availability, but also by air temperature. Temperature had a negative influence on feeding on mature leaves and fallen seeds, and a positive one on feeding on seeds and fruits (Fig. 1.3). Apparently in winter, while availability of fruits was highest, time spent feeding on fruits was lower (Fig. 1.2). At lower air temperatures, monkeys need to use more energy to maintain their own body temperatures (e.g. Nakayama *et al.*, 1971). When Yakushima macaques feed on fruits, they have to move for a long time, because fruits have a more dispersed distribution than other foods. However, Yakushima macaques can only move and feed for about 7 hours in a day (Agetsuma, in press), so it would be difficult to compensate for the greater energy requirement at lower temperatures simply by feeding on fruits. Therefore, they shifted to their feeding to foods which need less cost to be fed on, such as mature leaves, in winter.

The highly significant positive correlation between feeding on insects and temperature (Table 1.4) may reflect both increased activity of insects and larger populations at higher temperature. Insect feeding was also negatively correlated with feeding on mature leaves and
fallen seeds, and positively with feeding on fruits and seeds (Table 1.3).

Thus, temperature may influence dietary selection both directly and indirectly. Two mechanisms by which temperature influences dietary selection can be possible. One is through its influence on the energy required for thermoregulation. Within the variation of temperature in the study area (5-31 ° C), generally, the lower the

temperature becomes, the more energy the monkeys need for thermoregulation (e.g. Nakayama et al., 1971). Heat production of Japanese monkeys at 5 ° C is about 2.5 times greater than at 30° C (Nakayama *et al.*, 1971). Therefore, at low temperatures they feed on foods which require less energy to find, such as fallen seeds and mature leaves. By contrast, at higher temperatures, the monkeys need relatively less energy for thermoregulation, and also they can pursue higher quality, but more widely dispersed food items, such as seeds and fruits, by expending more energy in foraging.

Another mechanism is the influence through possibility of capture of insects as a protein source. Insects and mature leaves are probably the main protein sources for Yakushima macaques. In general, mature leaves contain higher protein and lower energy than fruits (Milton, 1993). When the temperature is high, and many insects are available, monkeys can depend on insects as a protein source, and on fruits and seeds as an energy source. On the other hand, at lower temperatures when insects are less available, monkeys have to feed on leaves for long periods to obtain their protein requirement. In fact, time spent feeding on insects was positively correlated with feeding on fruits ($r=0.42$, NS) and seeds ($r=0.67$, $p<0.05$), and negatively correlated with feeding on mature leaves ($r=-0.59$, $p<0.1$, Table 1.3).

These two mechanisms are not exclusive and it is possible that both influence dietary selection by Yakushima macaques to some extent.

It may be said that in general, animals who need more energy and/or protein, such as species with heavier body weight (Cultton-Brock and Harvey, 1977; Sailer *et al.*, 1985), pregnant or lactating females (Portman, 1970; Gautier-Hion, 1980; Harrison, 1983), monkeys in cooler habitats (Iwamoto and Dunbar, 1983), or in cooler seasons, as shown in this study, tend to have more folivorous diets.

Chapter 2

Foraging strategies of Yakushima macaques

2.1 INTRODUCTION

Many primate species show large seasonal variations in diets (Chapman and Chapman, 1990). Foods vary in their physical characteristics, nutrient contents and spatial distribution in the habitat (e.g. Clutton-Brock and Harvey, 1977; Harrison, 1984). This means that the foraging costs, in terms of searching and processing, and the nutritional benefits obtained, will differ between different food items. Monkeys must manage the allocation of time to feeding, moving and other behaviors in order to balance the costs and benefits of foraging on different food items. Therefore, their activity budget will be strongly influenced by the nature of the diet (Maruhashi, 1981; Marsh, 1978; Harrison 1985).

Clutton-Brock and Harvey (1977) examined inter-species differences in the relation between activity budget and diet in primates. They found a negative correlation between time spent feeding on leaves and both feeding time and moving time. They suggested that this was because foods other than leaves, such as fruits, flowers and animal matter, are generally less abundant in the forest and more time is needed for searching for and processing them.

A close relationship between activity budget and diet should be apparent for any primate species with a variable diet, but rather few studies have concentrated on this aspect (e.g. Marsh, 1981; Watanuki and Nakayama, 1993). In order to discuss species-specific feeding strategies, an understanding of the relationship between activity budget and diet is essential.

Foraging strategies of primates can be examined by assuming that distance moved, or time spent moving, represent the costs of foraging, while time spent feeding on foods such as fruits, which contain more energy than other foods, represent the benefits (Harrison, 1985; Agetsuma and Noma, in press). This paper examines the relationship between activity budget and diet in one group of Yakushima macaques. The findings are then discussed with reference to their foraging strategy.

2.2 STUDY AREA AND SUBJECTS

The study was carried out on the northwest coast of Yakushima (30 ° N, 131° E), an island in the south of Japan. Annual rainfall is about 2600 mm and mean temperature is 21° C. The area is covered by primary and secondary warm temperate broad-leaved forest. The diversity of plant species in the forest is very high (Tagawa, 1980), although 25 % of high trees (> 15 cm DBH) consisted of species of the Fagaceae and Lauraceae (Maruhashi, 1980).

Yakushima macaques (*Macaca fuscata yakui*) are one of two subspecies of Japanese macaques (*M. fuscata*) and are found only on Yakushima island, Japan. They feed mainly on fruits, seeds, leaves, flowers and insects (Maruhashi, 1980; Hill, 1991a). The composition of their diet is highly variable, both seasonally (Hill, 1991a) and inter-annually (Hill and Agetsuma, in press). The only report on their activity budgets is for the period from August to December (Maruhashi, 1981), when the composition of the diet is relatively stable.

2.3 METHODS

Observation of monkeys

Behaviors of Yakushima macaques in a well-habituated group (P Group: Hill, 1991b) were observed intermittently from January 1990 to May 1992. The group size varied from 5 to 19 members (including 2 to 6 adult males, 2 to 5 adult females), as a result of births, deaths and migration by males. Every 10 minutes the study group was scanned for 5 minutes and the behavior of all visible members of the group, excluding a suckling infant, were recorded (Altmann, 1974).

Food items, i.e. species and parts of woody plants, herbs, ferns, fungi, insects

and other items that the monkeys fed on, were also recorded. Trees that the monkeys fed from during scans were marked, as far as possible, between scanning periods.

Data analysis

Behaviors were classified into the following 5 activity categories. Feed: searching for, processing, and eating food items; Move: walking, running, climbing and jumping on the ground and trees; Social groom: grooming and being groomed by other monkeys; Inactive: sitting, lying, standing without any motion; Other activities: self-grooming, mounting and being mounted, agonistic behaviors. Feeding and moving were regarded as active behaviors in the analysis.

The analysis compares data from half-monthly periods because previous work on Yakushima macaques has shown that dramatic changes in the activity budget and diet can take place within a month (Hill and Agetsuma, in press).

The time spent in each activity was calculated using the following method. First, the number of monkeys engaged in each activity in each scan was calculated as a proportion of the total number of individuals in the scan. This was done to avoid over-representation of highly visible activities between each scan (Maruhashi, 1981; Harrison, 1985; Agetsuma and Noma, in press). For each half-month period, these proportions were then summed and divided by the total number of scans to give an average proportion for that activity.

Seasonal variation in day-length at the study site is more than 4 hours, and this is bound to influence the activity period of these diurnal monkeys. To control for this, the average proportion for each activity was multiplied by the mean day-length of all observation days within each half-month period.

Food items eaten by the monkeys were classified into seven categories according to their spatial distribution and nutritional characteristics, as follows. Fruits: whole fleshy parts of fruit with or without seeds; Seeds: seeds and nuts on trees,

excluding fallen seeds; Fallen seeds: fallen nuts, seeds and dried fruits in the leaf litter on the forest floor; Flowers: petals and nectar; Mature leaves: leaves completely unfurled; Young leaves: immature leaves, buds and new shoots; Insects: insects and the other animal matter; Fungi: toadstools, etc.

Time spent feeding on each food category was determined as a proportion of the total number of feeding records for each half-month period.

Vegetation survey

Densities and crown areas of food-tree species in the study area and crown areas of marked food-trees were surveyed from October, 1989 to February, 1993. Ninety eight 5m × 50m belt transects (total 2.45 ha) were established uniformly over an area of about 30 ha where the study group mostly ranged. The following method was used to estimate the crown area of all trees equal to or greater than 5 cm DBH, which lay on the transect belt. First, a line was measured that corresponded to the crown width at its greatest point (A). Then a second line (B), which was perpendicular to the first, was measured. The crown area was expressed as the area of an ellipse with long axis (A) and short axis (B). This method produces an estimate of actual crown area which can be used to compare different species at one location or in different locations (Agetsuma and Noma, in press).

The density of *Ficus superba* was too low to be surveyed by the belt transects, though the fruit is an important food item for the monkeys (Maruhashi, 1980, 1986). The number of trees of this species was determined over the entire 30 ha area and the crown areas of all trees were measured.

Crown areas of marked food trees were measured as far as possible by the same method as mentioned above, if they had not already been measured in belt transects.

The period of availability for each plant food item was assessed while making

observations of the monkeys and doing the vegetation survey. If at least one individual of a species bore a particular food item (i.e. fruits, seeds, flowers, mature leaves or young leaves) during a particular calendar month, then that food was recorded as being available in that month.

2.4 RESULTS

Activity budget

Twenty-two sets of half-monthly data on diet and activity budget were collected. For each half-month between 68 and 359 scan samples were taken. Data collection was done intermittently, but data were obtained during each of the four seasons.

Figure 2.1 shows seasonal changes in time spent feeding and time spent moving. Both feeding and moving time varied greatly. Feeding time was longer from December to May and shorter from June to November in general. Moving time showed the opposite trend to feeding time.

Mean and standard deviation (SD) of time spent in each activity in each of the 22 half-months were calculated (Table 2.1). Time spent in each activity was highly variable. However, time spent in active behaviors, that is the sum of feeding time and moving time, was rather more stable than either feeding time or moving time alone. The coefficient of variation (CV: SD/mean) for time spent in active behaviors was smaller than for those for feeding time or moving time (Active behavior-Feeding, $F=3.67$, $p< 0.01$; Active behavior-Moving; $F=3.47$, $p< 0.01$, $n1=n2=22$).

If it is assumed that monkeys remain inactive throughout the night, then the total inactive time in a 24 hour period can be calculated by summing time spent inactive during the day and night length. SD and CV for total inactive time were rather smaller than those for time spent inactive during daylight hours (SD, $F=1.73$,

$0.2<p< 0.3$, NS; CV. $F=60.4$, $p< 0.001$, $n1=n2=22$).

Diet

Seventy four species of woody plants and vines, and various kinds of herbs, ferns, insects and fungi were fed on by the monkeys. The monkeys ate the fruits of various species, including *Ficus superba, F. erecta, Myrica rubra,* and *Persea thunbergii,* the seeds of *Rhus succedanea,* and the mature leaves of species such as *Oreocnide pedunculata, Trema orientalis* and *Callicarpa* spp. Most of the fallen seeds fed on by the monkeys were the acorns of *Lithocarpus edulis.* The main flower-food species was *O. pedunculata.*

Time spent feeding on each food category is shown in Table 2.2. It can be seen that there was extreme variation in the diet. Each of fruits, seeds, fallen seeds, flowers, mature leaves and young leaves reached a maximum of at least 30 % of all feeding time in some half-months. Insects and fungi were rather supplementary foods, accounting for at most 25 %, and 8% of feeding time, respectively.

Correlations between feeding on each category and activity budget

Even in the same half-month, activity budget and diet could vary greatly between years. For example, late February in 1990, monkeys fed mainly on fallen seeds (38 % of feeding time) and on mature leaves (29 %), and spent feeding per day an average 5.3 hours. On the other hand in late February 1991, they fed mainly on mature leaves (62 %) and less on fallen seeds (1 %), and spent only 3.6 hours per day feeding.

There were several significant correlations between time spent feeding on each food category and time spent in each activity. Feeding on fruits, seeds, insects and fungi showed negative correlations with feeding time and significant positive correlations with moving time (Fig. 2.2).

The opposite trend was seen in time spent feeding on mature leaves, flowers, fallen nuts and young leaves, all of which were positively correlated with feeding time, and negatively correlated with moving time.

Correlations between feeding on each food category and time spent inactive were very similar to those with time spent moving (feeding on fruits, $r=0.28$; seeds, $r=0.37$; NS; insects, $r=0.69$, $p<0.001$; fungi, $r=0.47$, $p<0.05$; mature leaves, $r=-0.30$; young leaves, $r=0.22$; flowers, $r=-0.42$; NS; fallen seeds $r=-0.69$, $p<0.001$). This may be because inactive time was positively correlated with moving time ($r=0.54$, $p<0.01$). Total time spent inactive, time spent in active behaviors (feeding plus moving time) and time spent social grooming were correlated only weakly with feeding on each food category (total inactive, correlation coefficients ranged from -0.14 to 0.19; active behaviors, from -0.18 to 0.29; social grooming, from -0.29 to 0.40; NS).

Availability of food trees

Crown areas of 4 food trees or more were measured for 28 foods. The 28 foods (22 species) accounted for 52 % of feeding time and more than 70 % of feeding time on identified green plant-food excluding fallen seeds on average over 22 half-months. Mean crown areas of food trees of each item are shown in Table 2.3.

The mean crown area of food tree species, such as *Symplocos glauca, Oreocnide pedunculata, Ficus erecta, Trema orientalis, F superba japonica,* tended to be equal or smaller for leaf-food trees than for fruit-food trees of the same species (Table 2.3), although the difference was significant only for *Ficus erecta* (Mann-Whitney U test, $p < 0.01$, $n1=20$, $n2=8$). This tendency may reflect the fact that leaves can be obtained from trees of any size, whereas fruits can be obtained only from mature trees.

The density of food trees in the range of the study group was investigated (Table 2.3). The density of potential food trees for each food species was taken to be

the density of trees with a crown area larger than the mean. Food tree densities varied greatly across foods. Mean density of seed-food trees was 2.7 per ha (n=5), that of fruit-food trees was 3.6 (n=10), and that of mature leaf-food trees was 5.7 (n=10), although the differences between them were not significant (Mann-Whitney U-test, $p > 0.05$). However, the period of availability for mature leaf-foods tended to be longer than that for fruit- or seed-foods (mature leaf-seed, $p < 0.005$, n1=10, n2=5; mature leaf-fruit $p < 0.005$, n1=n2=10; Table 2.3). Therefore, in general, the density of trees with available food would be greater for mature leaf-foods than for fruit-foods or for seed-foods at certain times of year in this forest.

2.5 DISCUSSION

Correlation between activity budget and diet

Two types of correlation between food category and activity budget were found in Yakushima macaques. Time spent feeding on fruits, seeds, insects and fungi in the diet showed highly positive correlations with time spent moving and negative correlations with feeding time (Fig. 2.2). Densities of potential fruit-food trees and seed-food trees were lower in the forest (Table 2.3), so the monkeys had to spend more time moving to search for them. Insects may be scarce and evenly distributed compared to plant food, and be found and fed upon opportunistically by the monkeys. It could be that when they were looking for fruits or seeds, but could find none, they fed on insects along the way. In this case, it is obvious that feeding on insects would be positively correlated with time spent moving, as this would lead to increased opportunities to find these foods. Feeding on fungi showed a very similar trends to feeding on insects in relation to feeding time and moving time. The distribution of fungi may be similar to that of insects in the forest.

By contrast, time spent feeding on mature leaves, flowers, fallen seeds and

young leaves was inversely correlated with time spent feeding and moving. When the monkeys feed on these foods, they may have to spend more time foraging without moving. When the monkeys ate leaves, they had to eat for a long time to get enough energy, and spent little time moving, since leaves tend to contain more fiber and less energy than the other categories (Iwamoto, 1982; Chapman and Chapman, 1990). The main flower species eaten by monkeys was *O. pedunculata*, whose inflorescence is very small (about 3 mm). Processing this food was therefore time-consuming. Fallen seeds accounted for a very high proportion of feeding time in late winter. In this period, monkeys had to search intensively for the seeds of *L. edulis*, as they were dispersed and hidden in the leaf litter on the forest floor.

Time spent feeding and moving have been considered to be influenced by nutrient content, spatial distribution (Oates, 1987) and the need for manipulation of the food item (Clutton-Brock and Harvey, 1977). The findings of the present study also indicated that foraging on foods which have a low energy content with dense distribution (mature leaves), or which need much manipulation to be processed (flowers and fallen seeds) increases feeding time, while foods for which monkeys must search intensively in the forest (fruits, seeds, insects and fungi) lead to longer moving time.

The positive correlation between time spent feeding on leaves and total feeding time appears to conflict with the findings of Clutton-Brock and Harvey (1977) Using data from studies of several primate species, they found a weak negative correlation ($p < 0.1$) between time spent feeding on mature leaves and total feeding time. They concluded that this was because foliage is more abundant and requires less time for manipulation than other foods. This may be because they included in their analysis some specialized leaf-eaters, such as Colobinae species, which have the ability to digest highly fibrous foods (Sakaguchi, *et al.*, 1991). These monkeys may be able to obtain their nutrient requirements from a smaller amount of fibrous foods,

giving a shorter feeding time, than other monkeys. However, for individual species digestion rate tends to decrease as fiber content of food increases (Milton and Demment, 1988; Iwamoto, 1988, Sakaguchi *et al.,* 1991). Therefore, monkeys should spend more time feeding on leaves than on other foods.

Foraging strategies of Yakushima macaques

Seasonal changes were found in the activity budget of Yakushima macaques. However variations in activity budget within the same month were also large (Fig. 2.1). Monkeys tended to spend longer moving in the summer and feeding in the winter. While time spent feeding and time spent moving both had quite high coefficients of variation, time spent in active behaviors (i.e. the sum of the two) was relatively stable (Table 2.1). This suggests that monkeys are able to search and feed for only about 7 hours a day. This may reflect some kind of physiological limitation, such as time required for digestion, or the need to relieve fatigue. Therefore, the allocation of limited foraging time into feeding time and moving time in a day should be a critical factor in the monkeys' foraging strategy. Inactivity in a day time was positively correlated with time spent moving. This suggests that when monkeys move for longer, they must also rest for longer in a day time.

Monkeys adapted moving time to distribution pattern of their foods (Fig. 2.2 and Table 2.3). When they fed on leaves which densely distributed in the forest, they moved less. On the other hand, when they fed on fruits or seeds which distributed dispersedly, they moved longer. The higher cost of long moving time could be compensated for by the high energy contents of the fruits and seeds (Watanuki and Nakayama, 1993).

Harrison (1985) examined foraging strategies of green monkeys (*Cercopithecus sabaeus*) in terms of energetic costs and benefits of foraging behavior. He took day-range length to represent the energetic cost of searching for food, and

time spent feeding on fruit and flowers, which contain more readily-available energy than other foods (Harrison, 1984), as benefit. In this paper, I examined the foraging strategy of Yakushima macaques regarding feeding on fruits, which have more energy than mature leaves and may require less manipulation than flowers and fallen seeds, as benefit, and moving time as cost (Agetsuma and Noma, in press). Then, the positive correlation between fruit-feeding and moving time (Fig. 2.2) suggested that, when Yakushima macaques got high quality foods, they spent more time moving (i.e. high-cost high-yield; Harrison 1985), whereas when they were eating lower quality foods, they economized on the costs of moving (i.e. low-cost low yield).

Strategies similar to that found in the present study have been reported as a "high-cost high-yield" strategy and "low-cost low-yield" strategy in *C. sabaeus* (Harrison, 1985), a "loss-cutting policy" in *Hylobates syndactylus* and *H. lar* (Raemaekers, 1980), a "high cost / high reward" strategy in *Cebus* spp. (Terborgh, 1983 as cited by Brown and Zunino, 1990) and, "low-cost low-benefit" strategy in *M. f. fuscata* in cold temperate deciduous forests (Nakagawa, 1989). Thus, "balancing" the costs of foraging with the benefits of energy gains seems to be a common strategy employed by primates.

However, Raemaekers (1980) and Harrison (1985) pointed out that some primate species, such as baboons (e.q. Altmann and Altmann, 1970; Oliver and Lee, 1978) and vervet monkeys in Kenya (Wrangham and Waterman, 1981), may employ the opposite strategy, although a negative correlation between time spent feeding on fruits and moving time was not tested for. Which foraging strategy a primate uses will depend on a variety of factors, both environmental, such as food quality, availability, and distribution, and physiological, such as rate of metabolism, digestive ability, and tolerance of starvation. In order to determine the general principles governing primate foraging strategies it is necessary to take all of these factors into account.

Chapter 3

Rapid shifting of foraging pattern by Yakushima macaques as a reaction to heavy fruiting of *Myrica rubra*

3.1 INTRODUCTION

Animals change their feeding and ranging behaviors depending on food conditions in their habitat (Oates, 1987). Foraging patterns in some primate species have been regarded as strategies that lead to efficient nutritional intake in response to variation in the availability of different food resources (Harrison, 1984, 1985; Nakagawa, 1989 b; Watts, 1991). It has been reported that aspects of foraging behavior, including food choice, activity budget, travel distance and range-use of many species of primates are affected by food availability, quality and spatial distribution (Clutton-Brock, 1975; Raemaekers, 1980; McKey and Waterman, 1982; Harrison, 1983, 1984, 1985; Estrada, 1984; Vedder, 1984; Sugardjito *et al.*, 1987; Nakagawa, 1989 b; Brown and Zunino, 1990; Chapman and Fedigan, 1990; Lucas and Corlett, 1991; Stanford, 1991). Most studies have focused on monthly variation in foraging patterns. However, Harrison (1985) suggested that green monkeys may change their patterns of foraging within much shorter periods in relation to changes in the relative costs and benefits of foraging on different foods. If food conditions in a habitat vary greatly within short periods, animals should change their foraging patterns accordingly to maximize foraging efficiency. To reveal such a close relationship between variability of foods and foraging pattern, short term studies are needed.

This paper reports short term shifts in the foraging patterns of wild, free-ranging Yakushima macaques (*Macaca fuscata yakui*) in a warm-temperate forest. These shifts are discussed in relation to changes in the availability of *Myrica rubra* fruit, which was the macaques' main food source during the study period.

3.2 STUDY AREA AND SUBJECTS

The study was carried out on the island of Yakushima (30° N, 131° E), in the southwest of Japan. The study area is located at the foot of Mt. Kuniwaridake (alt.

1323m), in the western part of the island, between 0 and 250m above sea level. The annual mean temperature is 21° C and the mean annual rainfall is about 2600 mm. This area is covered with warm-temperate broad-leaved forest. The canopy layer consists of species mainly belonging to Fagaceae, Lauraceae, Myrsinaceae and Theaceae, but there is no predominant tree species in the forest (Tagawa, 1980). The trees rarely exceed 20m in height, because of the frequent occurrence of strong winds and typhoons. The study area contains various types of vegetation: primary forest, mixed primary and secondary forest, patches of early successional deciduous trees along the road, and coastal vegetation.

Yakushima macaques are one of two subspecies of Japanese macaques (*Macaca fuscata*) and are found only on Yakushima. They feed mainly on fruits, seeds, leaves, flowers and insects (Maruhashi, 1980). The composition of their diet varies seasonally, and is especially variable from December to June (Hill 1991 a).

3.3 METHODS

Availability of *Myrica* fruit

Myrica rubra fruit was the most important food during the study period. The crop sizes of seven individual trees in the study area were estimated four times from May 9-17, May 22-25, June 5-6, and on June 23, 1990.

Color of *M. rubra* fruit changes from green (unripe), through orange (semi-ripe) to red (ripe). The number of each colored fruit was counted directly on sample branches. The crop size of each tree was estimated by dividing the number of fruits counted by the proportion of the whole crown volume that the sample branches represented.

Survey of vegetation

Vegetation of the study area was surveyed from September, 1990 to May, 1992. Thirty quadrats, each of one hectare, were marked in the study area. In each of these 30 quadrats, one to four 5m × 50m belt transects were established. The following method was used to estimate the crown area of all trees equal to or greater than 5 cm DBH, which lay on the transect belt. First, a line was measured which corresponded to the crown width at its greatest point (A). Then a second line (B) which was perpendicular to the first was measured. The crown area was expressed as the area of an ellipse with long axis (A) and short axis (B). This method produces an estimate of actual crown area which can be used to compare different species at one location, or a single species at different locations.

Estimated crown areas were summed for each species and divided by the total transect area to give a measure of crown density. The diversity of species whose leaves were fed on by the monkeys in the study period was expressed by Shannon's formula (Pielou, 1966), calculated from the proportion of crown areas of each leaf-food species to total crown area of leaf-food species in each quadrat.

Foraging behavior

Behaviors of a single habituated group of Yakushima macaques (P group; Hill, 1991b) were observed from May to June, 1990. Eighteen to nineteen monkeys belonged to the group: 5-6 adult males, 5 adult females, and 8 immatures including 1 infant.

Every 10 minutes a 5-minute scan (Altmann, 1974) was made during which the behavior and location (quadrat No.) of all visible members of the group, excluding a suckling infant, were recorded. The term "record" is used below to refer to data for one individual for one scan. Food items, i.e. parts and species of woody plants, herbs, ferns, fungi, insects and other items which monkeys fed on, were also recorded.

Travel distances of the group were recorded on maps and measured every observation day.

Data analysis

Behavioral data were analyzed in each of the four 10-day periods based on the date of counting of *M. rubra* fruit on sample trees: May 5 to 14 (Period 1), May 20 to 29 (Period 2), June 5 to 14 (Period 3), June 20 to 29 (Period 4). The numbers of scans conducted in Period 1, Period 2, Period 3 and Period 4 were 190, 160, 188 and 216, respectively. The mean number of animals observed in one scan was 9.5 +/- 3.0 (s.d.).

Time spent feeding on each food item was determined from the number of records of feeding on that food item, as a proportion of the total number of feeding records in each 10-day period. The diversity of food items in the diet for each period was expressed by Shannon's formula (Pielou, 1966).

The time spent in each activity was calculated using the following method. First, the number of monkeys engaged in each activity in each scan was calculated as a proportion of total number of individuals in the scan. This was done to avoid over-representation of highly visible activities during each scan (Maruhashi, 1981; Harrison, 1985). For each scan the proportion of animals observed in a particular activity was calculated. For each 10 day period, these proportions were then summed and divided by the total number of scans to give an average proportion for that activity.

The mean travel speed was calculated from the total travel distance of the study group in each period divided by total observation time for that period.

To examine intensity of range-use, the number of records of individuals observed in a particular quadrat was calculated as a proportion of the total number of records of individuals for each period.

3.4 RESULTS

Quantity of *Myrica rubra* fruit

Figure 3.1 shows changes in the estimated number of fruit on seven *M. rubra* trees throughout the study period. Total numbers of the fruit on the trees began to decrease between late May and the beginning of June. The rate of decrease accelerated in mid-June.

Matured red fruit of *M. rubra* were found beginning May 21st during observations of monkeys in the forest. However, the beginning of the ripening period varied over a few weeks according to the location of the trees in the forest and among individual trees of the same location. The semi-ripe fruit on the sample trees were found beginning in late May. The ripe fruit on the trees should increase considerably from late May to the beginning of June.

Dietary composition

Throughout the four periods the monkeys were observed feeding on 24 species of woody plant including leaves and buds of 19 spp, fruits of 7 spp, flowers of 1 sp, and unidentified parts of 1 sp. They also ate several species of herbs, ferns, fungi, insects and other items. Composition of the diet was examined using four main food categories: *M. rubra* fruit, other fruits, leaves and buds, and insects (Fig. 3.2). There was a significant difference in the proportion of each food category in their diet between the four periods (Pearson Chi-square = 758, df=9, $p<0.001$).

Forty percent of feeding in Period 1 was on leaves and buds of 17 woody plant species including *Daphniphyllum teijsmannii, Ficus erecta, Trema orientalis, Callicarpa* spp, and *Oreocnide pedunculata.* However, in the following periods, less than 3.5 % of feeding was on leaves and buds.

The percentage of feeding on *M. rubra* fruit increased considerably in Period 2 when the fruit began to ripen. After Period 2, feeding on the fruit decreased.

Monkeys fed not only on ripened fruit and semi-ripened fruit, but also on unripe fruit to some extent.

By contrast, the percentage of feeding on the other fruits, such as those of *Persea thunbergii* and *Ficus erecta,* decreased gradually in Period 2, and then increased in the following periods.

Total time spent feeding on fruits were 38.6 % in Period 1, 84.7 % in Period 2, 73.8 % in Period 3 and 56.1 % in Period 4. Each of the top 3 fruit-food species, and the top 5 leaf-food species exceeded 1 % of feeding time on average over the four periods. Insect-eating was observed frequently in the latter two periods. Food items in the diet of Period 1 were highly diversified. However, dietary diversity dramatically decreased in Period 2, and then gradually increased.

Activity budget and Mean travel speed

The activity budget was considerably different between the former and the latter two periods (Fig. 3.3), and a drastic change in dietary composition occurred between Period 1 and Period 2 (Fig. 3.2). Time spent feeding in the former two periods was about twice that of the latter two periods. Time spent moving was greater in the latter two periods, though the difference was rather small in contrast to that of time spent feeding. Mean travel speed increased gradually from early May to late June, while dietary composition and activity budget changed drastically (Fig. 3.3).

Ranging pattern and vegetation

P group ranged over about 31 hectares during the study period. For each period more than 89 percent of scan records were from quadrats included in the vegetation survey. Ranging patterns of monkeys was considerably different between Period 1 and Period 2 (Fig. 3.4) corresponding to the change of dietary composition (Fig. 3.2).

In Period 1, monkeys ranged in the north-western and south-eastern parts of the study area. In Period 2, monkeys intensively ranged over the western part. More than 30 % of records were from only one quadrat (A4) in this period. In Period 3 and Period 4, monkeys ranged more evenly around the western part.

Coefficients of variation of crown density of *M. rubra, P thunbergii* and *F. erecta* in each quadrat were 1.59, 1.27 and 0.69, respectively (n = 30). Thus, the top 2 fruit-food species, other than *M. rubra,* were distributed more evenly than *M. rubra* (Fig. 3.5a and b). The crown density of *M. rubra* was highest in the western part of the area.

The top 5 leaf-food species were distributed rather densely in the southern part of the area (Fig. 3.5c). However, diversity of all leaf-food species in each quadrat was higher in the northern part along the streams and road where natural and artificial disturbances of vegetation were likely to occur (Fig. 3.5d).

In Period 1, there were no significant correlations between the use of each quadrat and the density of *M. rubra,* of the other top 2 fruit-food species, or of the top 5 leaf-food species in each quadrat (Spearman rank correlation tests, *M. rubra,* rs=-0.01; other fruits, rs=0.07; leaves, rs=0.14; N=30; n.s.). However, there was a significant positive correlation between use of quadrats in Period 1 and diversity of leaf-food species (total of 19 spp) in the quadrats ($rs=0.38$, $p<0.05$). Range-use in each of the three periods from Period 2 to Period 4 was positively correlated with the density of *M. rubra* (Period 2, $rs=0.39$, $p<0.05$; Period 3, $rs=0.35$, $p<0.1$; Period 4, $rs=0.49$, $p<0.01$; N=30). In contrast, there were negative correlations between the use of quadrats and the density of the top 5 leaf-food species in the quadrats from Period 2 to Period 4 (Period 2, $rs=-0.37$, $p<0.05$; Period 3, rs=-0.03; Period 4, rs=-0.23; n.s.; N=30).

3.5 DISCUSSION

The study group rapidly changed their foraging patterns in relation to the availability of *Myrica rubra* fruit. Before the ripening of the fruit (Period 1), the monkeys moved slowly and spent much time feeding on the leaves and buds of many species. In this period, they ranged mainly in those quadrats which showed higher leaf-food species diversity. When *M. rubra* fruit began to ripen (Period 2), the monkeys fed intensively on them, though their activity budget did not change. They shifted their range to the southwestern part of the study area, where *M. rubra* trees were densely distributed. The monkeys were able to obtain many fruits without moving far while the fruits were abundant. As total number of the fruit decreased (Period 3 and Period 4), the monkeys gradually shifted to insects and other fruits which were distributed more evenly. They spent more time moving, moved at higher speeds and ranged more evenly, presumably in order to find these foods.

It has been suggested that monkeys diversify their diet in order to avoid the accumulation of secondary compounds, and/or to promote efficiency of digestion (Hladik *et al.*, 1971; Coelho *et al.*, 1976; Marsh, 1981; Estrada, 1984; Harrison, 1984). When monkeys feed frequently on leaves which have more undigestible fibers and secondary compounds than other foods (McKey, 1974; Waterman, 1984), it is expected that they will diversify their diet to improve nutrition intake efficiency. The foraging pattern found in Period 1 suggests that when they fed on leaves frequently, they diversified their diet by ranging in areas where many leaf-food species were available.

Foraging strategies of the monkeys were examined in terms of the costs and benefits of foraging. The benefit of foraging should be expressed as total nutrition intake (Iwamoto, 1982; Nakagawa, 1989 a). However, it is difficult to detect accurate intake masses, nutrition contents and digestion rates of each food item in the field. In this study, the costs were expressed as distance moved, or time spent moving, and

benefits in terms of time spent feeding on fruits, which generally contain more energy than other foods, following Harrison (1985) and Agetsuma (in press).

Before the ripening of *M. rubra* fruits, the monkeys employed a "low-cost, low-yield" strategy (Harrison, 1985). When the fruits began to ripen they shifted to a "low-cost, high-yield" strategy, which would be the most beneficial. As the number of *M. rubra* fruit decreased, monkeys shifted to a more costly strategy with minimum reduction in time spent feeding on fruits. The benefits in Period 3 and Period 4 were intermediates between those in Period 1 and Period 2. However, the benefits in these periods might not be comparable with those in the former two periods, because the feeding time was very different.

Agetsuma (in press) reports that in general, the more fruits Yakushima macaques forage on, the more time they spend moving. This was interpreted in terms of balancing the cost of moving against the benefit of a high-energy food resource. However, in this study, when *M. rubra* fruit was abundant (Period 2) monkeys fed on the fruit intensively without a distinct increase in time spent moving or in travel speed (Fig. 3.2 and Fig. 3.3). This foraging pattern was, therefore, an exception to the basic pattern.

One possible explanation for this would be that the low energy content of immature *M. rubra* fruit meant that the monkeys had to feed for a long time in order to get enough energy. However, it seems unlikely that the monkeys would have shifted their range so drastically, from Period 1 to Period 2, in order to feed intensively on a low-energy food.

Another possible reason is that the abundance and spatial clumpedness of *M. rubra* fruit may enable monkeys to feed on the fruit intensively without moving for a longer time (Iwamoto, 1992). A similar foraging pattern was reported when Yakushima macaques fed on *Ficus superba* which also had abundant fruit at that time (Maruhashi, 1986). Thus, the "low-cost, high-yield" strategy, which seems to be the

most beneficial, may be possible only during periods when the fruit of certain species are available in abundance.

It has been reported that some primate species shift their foraging patterns (diet and range) to feed intensively on one preferred food item which is available for only a few months (Vedder, 1984; Lucas and Corlett, 1991). In this study, monkeys showed a drastic shift of diet, range and activity budget in a very short period. The ability to shift foraging patterns, especially to a "low-cost, high-yield" strategy, may be an effective means of maximizing feeding efficiency under highly variable food conditions.

One of the reasons why such a rapid and drastic shift of foraging pattern was found in Yakushima macaques may be strong intra-specific feeding competition. There are no arboreal mammalian frugivores other than monkeys in this forest. A high density of monkeys (Takasaki, 1981) with extreme range overlap between monkey groups (Hill and Agetsuma, in press) will increase the variability in food conditions. Most of the decrease in *M. rubra* fruit was due to the feeding of the monkeys during the study period. Several frugivorous birds, such as *Hypsipetes amaurotis* and *Sphenurus formosae* (Eguchi *et al.*, 1989), also fed on the fruit. Plant species which have a clumped distribution, and which bear abundant fruit for short periods are likely to attract other groups of monkeys and frugivorous birds. In fact, Hill and Agetsuma (in press) reported that when Yakushima macaques fed on *M. rubra* fruit, inter-group encounters occurred frequently in the place where *M. rubra* was densely distributed. To make the most of these resources the monkeys must be able to change their foraging patterns as soon as the fruit becomes available.

This ability of Yakushima macaques to effect rapid shifts in foraging patterns may be enhanced by the small size of their ranging areas. Yakushima macaques range over smaller areas than do other populations of Japanese macaques (Takasaki, 1981), or many other species of Anthropoidea (Milton and May, 1976). This may allow them

to monitor changes in the availability of various foods more closely than would be possible over a larger area, and to change their foraging patterns accordingly.

Further studies of other populations of Japanese macaques and other primate species are needed to be certain of the relationship between shifts in foraging patterns, and the variability of food conditions and the size of the ranging area.

Chapter 4

Foraging synchrony in a group of Yakushima macaques

4.1 INTRODUCTION

Individuals of many primate species forage together in groups. Groups with stable membership must have foraging patterns which enable all members to get their nutritional requirements. If this were not the case, then individuals who could not get enough food would have to leave the group (Kummer, 1971; Chapman, 1990) or die. This suggests that the foraging patterns of individuals within a group must allow for the foraging efficiency of other members to some extent. In this sense the foraging pattern of the group as a whole should maximize the mean and minimize the variance of food intake among group members.

Previous studies have shown that not all members of a feeding group optimize their foraging efficiency simply in relation to the availability of food resources (Maruhashi and Yumoto, 1990; Nakagawa, 1990; Grether, *et al.*, 1992). Maruhashi and Yumoto (1990) showed that one Yakushima macaque (*Macaca fuscata yakui*) in a group travels about 1 km a day, and encounters about 33 food patches. However, the monkey actually forages in only about 10 of these patches, and so would not need to travel 1 km for his own foraging needs alone. Nakagawa (1990) and Grether, *et al.* (1992) studied food patch use by *M. fuscata fuscata* and *Hylobates* species, respectively. Neither study found evidence that individual monkeys in a group optimize their own foraging efficiency in a food patch. This may be regarded as one of the costs of group-living. Such costs may be offset by benefits of group-living, such as defense from predators, ability to compete with other groups of conspecifics for food, and greater access to potential mates (e.g. Dunbar, 1988; Fleagle, 1988).

In order to forage efficiently, the members of a feeding group should adjust their behavior in relation to both the activities other individuals and the availability of food resources (Kummer, 1971). Avoiding synchrony in foraging activity may be one way to minimize intra-group feeding competition (Harrison, 1985). However, synchrony of feeding behavior among individuals in a group is commonly found in

primates (e.g. Chivers, *et al.*, 1975; Kavanagh, 1978; Harrison, 1985). Approximate synchrony of behaviors is needed to gather members of a group in space (Kavanagh, 1978). Moreover, when the group encounters a particular high quality food which is limited in time or space, individuals would be expected to synchronize their feeding behavior (Kavanagh, 1978; Harrison, 1985). Individuals which do not join in will miss the opportunity to use the resource before the group moves on, or before the resource is completely consumed by other group members.

The degree and duration of synchrony of activity is therefore a very significant aspect of group-living in primates. This paper examines synchrony of activity in a wild group of Yakushima macaques (*Macaca fuscata yakui*). Firstly, the degree and duration of synchrony are considered in relation to group size and diet. Then, the relation between the duration of the active phase, when most members of the group are feeding and moving, and resource use is discussed.

4.2 STUDY AREA AND SUBJECTS

The study was carried out on the northwest coast of Yakushima island (30° N, 131° E) in Japan. The study site is in part of the area designated as Natural World Heritage, and is covered by primary and secondary warm-temperate broad-leaved forest. The canopy layer consists of species belonging mainly to the Fagaceae, Lauraceae and Myrsinaceae, but there is no predominant plant species in the forest (Tagawa,1980). Annual rainfall is about 2600 mm and mean temperature is 21° C.

Yakushima macaques are one of two subspecies of Japanese macaque (*M. fuscata*) and are found only on Yakushima island. They feed mainly on fruits, flowers, leaves and insects (Maruhashi, 1980). The composition of their diet varies seasonally (Hill, 1991a), and their activity budget also varies greatly with their diet (Agetsuma, in press).

4.3 METHODS

Observation of monkeys

Behaviors of Yakushima macaques in a well-habituated group (P Group: Hill, 1991b) were observed intermittently from February 1990 to March 1991 (Period 1) and September 1991 to April 1992 (Period 2; Table 1). Group size varied from 15 to 19 animals (large group) in Period 1, and from 5 to 8 (small group) in Period 2, as a result of births, deaths and migration by males.

The study group ranged over about 30 hectares (Hill and Agetsuma, in press). Ninety eight quadrats of 1/4 ha were marked out over about 25 ha of the range. Every 10 minutes a 5-minute scan (Altmann, 1974) was made during which the behavior and location (quadrat number) of all visible members of the group, excluding suckling infants, were recorded (Agetsuma and Noma, in press). Food items, i.e. species and parts of woody plants, herbs, fungi, insects and other items which the monkeys fed on, were also recorded. Trees which the monkeys fed from during scans were marked, as far as possible. The largest distance between visible monkeys (LD) was estimated in each scan.

Data analysis

Behaviors were classified into feeding, moving, resting, social grooming, self-grooming, and other activities. The monkeys rarely walked for long time without engaging in some other activity, such as feeding or searching for food. Feeding and moving were regarded as active behaviors while resting, social grooming and self-grooming were regarded as inactive behaviors (Harcourt, 1986). Agetsuma (in press) showed that feeding time and moving time vary greatly in relation to diet, however, the sum of the two, i.e. active behaviors, remains relatively constant. Their 'foraging

efforts' can therefore be measured by the sum of feeding and moving time for this analysis.

The analysis compares data from 14 half-months in the two periods (Table 4.1). The time spent in each activity was calculated using the following method. Only scans in which one third of the group members or more were observed were used. For each scan, the number of monkeys engaged in each activity was calculated as a proportion of the total number of individuals in the scan (Maruhashi, 1981; Harrison, 1985; Agetsuma and Noma, in press). For each half-month, these proportions were then summed and divided by the total number of scans to give an average proportion for that activity. Individuals in a group tend to synchronize their activity (Chivers *et al.*, 1975; Kavanagh, 1978; Harrison, 1985). Times when most individuals are feeding and moving can be regarded as the "active phase" of the group. In this study, the active phase was defined as any time when the proportion of active behaviors in the scans was more than the mean proportion of active behaviors in the half-month. Times when the proportion of active behaviors in the scans was less than the mean were defined as the non-active phase. Food items fed on by the monkeys were classified into 5 categories: 1) Fruits (including seeds) which were taken from the trees; 2) Leaves including shoots; 3) Flowers including nectar; 4) Fallen seeds including dry fruits in the leaf litter on the forest floor; 5) Insects and other animal matter.

Time spent feeding on each food category in each phase and in each half-month was determined as a proportion of the total number of feeding records for each phase and each half-month, respectively.

4.4 RESULTS

Time spent feeding on each food category Yakushima macaques fed mainly on fruits, leaves, flowers, fallen seeds and insects (Table 4.1). Monkeys fed on fruits

for more than 57 %, and leaves for less than 7 %, of feeding time in LMAY, EJUN, LJUN and EAUG of Period 1, and in LSEP, ENOV and EDEC of Period 2. These half-months are therefore referred to as the fruit-eating season. On the other hand, monkeys fed on fruits for less than 41 % of feeding time in LFEB1, EMAR, EMAY, LDEC and LFEB2 of Period 1, and LJAN and LAPR of Period 2. In each of these half-months, monkeys fed on leaves for more than 22 % of feeding time, and they are collectively referred to as the non-fruit-eating season in this study.

Degree of Synchrony

The mean number of animals observed in one scan was about 10 (range 9.2-10.5) in Period 1 and 5 (4.2-5.5) in Period 2. The activity budget of Yakushima macaques in each season is shown in Table 4.2. Time spent in active behaviors ranged from 45 to 75 %. Figure 4.1 shows the proportion of scans in which different percentages of the monkeys observed were engaged in active behaviors in each half-month. If the monkeys completely synchronized their activity, then all data would fall in the categories 0-20 and 81-100 %. On the other hand, if the monkeys behaved randomly, the histogram would show a binomial (normal) distribution with the value of active behaviors (Table 4.2) as the mean. In the histograms for Period 2, the frequency of categories 0-20, 61-80 and 81-100% were high (lower part of Fig. 4.1). Expected values of the binomial distribution can be calculated by supposing that the number of monkeys observed is 10 for Period 1, and 5 for Period 2, with the mean of active behaviors in each half-month. Then, in the categories 0-20 and 81-100 % for all half-month, observed values were greater than expected values (for both category: Sign test, $p < 0.01$, 14 pairs). For all half-month data of each scan were transformed to Z scores (Zar, 1984) for standardizing differences of the mean and variance between half-months. If the monkeys behaved randomly, Z transformed scores would be expected to show normal distribution. Then, the normality of the distribution in each

histogram was tested using a Kolmogorov-Smirnov test. For 7 out of 9 half-months in Period 1, and for all half-months in Period 2, there were significant differences from a normal distribution (Table 4.2). These results mean that monkeys did not behave randomly but tended to synchronize their activity to some extent.

To detect the degree of the synchrony, coefficient of variation (CV) of percentages of the monkeys engaged in active behaviors in each scan were examined in each half-month (Table 4.2). Higher values of the CV indicate greater synchrony of activity. The CV in Period 2 tended to be higher than Period 1 (Mann-Whitney U test, $p < 0.02$, n1=9, n2=5). Indicating that when the group was small the monkeys synchronized their activity more closely than when it was large. However, there was no significant difference between the fruit-eating and non-fruit-eating seasons ($p > 0.05$, n1=n2=7, NS).

Temporal spacing pattern and number of food items

The largest distance (LD) between visible monkeys in each scan is shown in Table 4.3. Data for Period 1, excluding LDEC and LAUG, were too few to analyze. LD during the active phases tended to be greater than during the non-active phases (Wilcoxon signed ranks test, $p < 0.02$, n1 = 7, n2 = 7).

LD of Period 1 tended to be greater than that of Period 2 (Mann-Whitney U test, p=0.053, n1=2, n2=5). However, LD during the fruit-eating seasons was not always greater than that of non-fruit season.

The mean number of food items in each active scan (Table 4.3) was higher in the non-fruit-eating season than in the fruit-eating season ($p < 0.005$, n1 = n2 = 7), although there was no significant difference between Period 1 and Period 2 ($p > 0.05$, n1 =9, n2 = 5, NS).

The duration of the active phase

For each half-month the proportion of all active scans, and of all inactive scans, which were part of a continuous phase of 40 minutes (i.e. 4 consecutive scans) or longer was calculated (Table 4.4). Phases which were less than 3 scans and which included the first or last scan of observations were omitted from the analysis. The proportion of active scans which were part of a continuous phase was greater in the non-fruit-eating season than in the fruit-eating season (Mann-Whitney U test, $p < 0.005$, $n1 = n2 = 7$). There was no significant difference between the proportion of the active scans that were continuous in Period 1 and in Period 2 ($p > 0.05$, $n1 = 9$, $n2 = 5$, NS).

There was no significant difference in the proportion of continuous non-active phases between non-fruit-eating and fruit-eating seasons ($p > 0.05$, $n1 = n2 = 7$, NS), or between Periods 1 and 2 ($P > 0.05$, $n1 = 9$, $n2 = 5$, NS).

The duration of the active phase and ranged area

Figure 4.2a shows the relation between the duration of the active phase and the range (number of quadrats) used during that phase. There were highly significant positive correlations between the duration of the phase and range area in the two periods, irrespective of the season (Period 1, $y=0.59x+1.1$, $r = 0.74$, $n = 185$, $p < 0.001$; Period 2, $y=0.18x+1.5$, $r = 0.47$, $n=71$, $p < 0.001$; these regression lines are not shown in Fig. 4.2a). However, the inclination of the regression line for Period 1 was more than 3 times greater than that for Period 2 ($t=-2.9$, $p<0.01$, $\upsilon=252$).

There were also positive correlations between the duration of the active phase in both the fruit-eating and non-fruit-eating seasons, and range area (Period 1, fruit-eating season, $y=0.83x+0.60$, $r = 0.84$, $n = 119$, $p < 0.001$, non-fruit-eating season, $y=0.34+1.57$, $r = 0.68$, $n = 66$, $p < 0.001$; Period 2, fruit-eating season, $y=0.20x+1.6$, $r = 0.49$, $n = 40$, $p < 0.01$, non-fruit-eating season, $y=0.18x+1.4$, $r = 0.48$, $n=31$, $p < 0.01$; Fig. 4.2a). In Period 1 the inclination of the regression line for the fruit-eating season was 2.5 times greater than that for the non-fruit-eating season ($t=6.8$, $p<0.01$,

υ=181), although in Period 2 the inclinations for the fruit- and non-fruit-eating seasons were almost the same (t=0.12, NS, υ=67).

The duration of the active phase and food trees

Correlation between the duration of the active phase and the number of food trees used during the active phase was tested for (Fig. 4.2b). There was a significant positive correlation between the duration of the active phase and the number of food trees used in both periods, irrespective of the season (Period 1, $y=0.67x+0.60$, $r = 0.65$, $n = 244$, $p < 0.001$; Period 2, $y=0.57x+0.64$, $r = 0.74$, $n=82$, $p < 0.001$; These regression lines are not shown in Fig. 4.2b). There was no great difference in the inclination of the regression lines between duration of active phase and food trees in either period (t=0.86, NS, υ=322).

The inclination of the regression line for the non-fruit-eating season ($y=0.72x+0.93$, $r=0.64$, $p< 0.001$, $n=125$) was 1.5 times larger than that for the fruit-eating season ($y=0.50x+0.56$, $r=0.68$, $p<0.001$, $n=119$) for Period 1 (t=1.9, $p<0.05$, υ=240). However, the regression lines for the fruit-eating season ($y=0.56x+0.52$, $r=0.72$, $p<0.001$, $n=51$) and non-fruit-eating season ($y=0.56x+0.94$, $r=0.74$, $p<0.001$, $n=31$) for Period 2 were almost the same (t=0.05, NS, υ=78).

Food items in the non-active phase

The percentage of all feeding records in each food category during the active phase and non-active phase are shown in Table 4.5. A significant difference in the percentage of fruit, and non-fruit foods was found between the active phase and the non-active phase in 8 of the 14 half-months. Time spent feeding on the top food category of the season decreased in the non-active phase in 10 out of 14 half-months. In the non-fruit-eating seasons, time spent feeding on leaves (6 out of 7 non-fruit-eating half-months) and that on fallen seeds (4 out of 7) tended to decrease, while time

spent feeding on fruits tended to increase during the non-active phase (5 out of 7). On the other hand, in fruit-eating seasons, feeding on fruits tended to decrease in the non-active phase (5 out of 7 fruit-eating half-months). In 11 out of 14 half-months, insect-eating increased in the non-active phase.

4.5 DISCUSSION

Degree of foraging synchrony

The current data show that behaviors of individuals were less synchronized when the group was large (15-19 individuals) than when it was small (5-8 individuals). A reduction in the synchrony of behavior in order to minimize food competition among group members (Harrison, 1985) might be expected in a larger group. Monkeys in a large group would have to find more food patches, and reduce competition over food, in order to get sufficient. Therefore, foraging patterns were strongly influenced by the distribution of foods and synchrony of behavior was low when the group was large. Fruit-food trees tend to be distributed more sparsely than other food trees (Agetsuma, in press). So, when the group was large it ranged over a wider area, but could feed on less food trees in the fruit-eating than non-fruit-eating seasons in the active phase (Fig. 4.2). By contrast, when the group was smaller, there was a much less clear relationship between food type, range area and the number of food trees used. Moreover, most of the members in a small group could feed on only a few food patches simultaneously.

However, if intra-group competition is more apparent when monkeys feed on foods which contain higher energy, and which are patchily distributed (Janson and Van Schaik, 1988, Nakagawa, 1994), then the degree of synchrony of behavior should be lower, and LD should be greater in the fruit-eating season, in order to reduce food competition. In fact, neither the degree of synchrony nor the largest distance between

visible monkeys in a scan (LD) were affected by food type (Table 4.2 and Table 4.3). Maruhashi (1986) showed that the length of a feeding bout for a Yakushima macaque was almost the same in a fruit-food patch as in a leaf-food patch. Therefore, from the idea of the marginal value model (Charnov, 1976), the quality of fruit patches and leaf patches may not differ for Yakushima macaques. It is also possible that the level of intra-group food competition is too low to affect synchrony of behaviors among group members, because Japanese monkeys tend to stop foraging before the depletion of a food patch (Maruhashi, 1986; Nakagawa, 1990).

Synchronization of behaviors is required for maintaining spatial cohesion between group members (cf. Kavanagh, 1978). It may be more important in a small group, because its members give fewer vocalizations, make less noise in general, and are less dispersed (Table 4.3) than those of a large group, and so would be more difficult to locate once a member became lost.

The duration of the active phase

The duration of the active phase depended on the type of food resource. In the non-fruit-eating season, monkeys fed on more food items, and in more food trees, over a smaller area per active phase than in the fruit-eating season (Table 4.3, Table 4.4 and Fig. 4.2b). Moreover, when Yakushima macaques feed a lot on leaves, they tend to range where many species of leaves are available (Agetsuma and Noma, in press). So, in the non-fruit-eating season, they could stay longer in a small area and still feed on a variety of species.

The difference in the duration of the active phase between the fruit-eating and non-fruit-eating seasons may be explained by a physiological mechanism. Compared with leaves, fruits tend to contain much higher proportions of easily-digested carbohydrates, such as sugar and starch (Milton, 1993). Therefore, fruit-eating is followed by a rapid rise in blood-sugar level. When the concentration of glucose in

the blood reaches a certain level, "the satiety center (ventromedial hypothalamic nucleus)" inhibits further feeding behavior (Morita and Kubota, 1982). Therefore, when monkeys feed on fruits, they may feel sated much more rapidly than when they feed on leaves.

Diet in the non-active phase

In the active phase the monkeys fed on major food items, and in the non-active phase, they fed on foods which are of higher quality, but which are more difficult to find. Fruits tend to contain more energy than leaves (Milton, 1993), but less protein than either leaves (Milton, 1993) or insects (Iwamoto, 1982). The density of fruit-food trees in the forest tended to be lower than that of leaf-food trees (Agetsuma, in press). Therefore, in the non-fruit-eating season, fruits were higher quality food in terms of energy, although the searching cost was high. However, if fruits were found opportunistically during non-active phases, they would be highly beneficial foods, and, indeed, the monkeys increased feeding on fruit during the non-active phase in the non-fruit-eating seasons (Table 4.5). Similarly, insects would be beneficial as a source of protein, especially in the fruit-eating seasons, when monkeys could find them opportunistically.

It has been suggested that to avoid secondary compounds and improve digestibility, primates should diversify their dietary intake (e.g. Hladik *et al.*, 1971; Coelho *et al.*, 1976; Marsh, 1981; Estrada, 1984; Harrison, 1984). Yakushima macaques may diversify their diet by feeding on foods other than the main food of the season during the non-active phase.

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Table 1.1

Types of common food items

	No. common items (main items)			
Food category	Type 1	Type 2	Type 3	Total
Young leaves	1 (1)	-	5 (1)	6 (2)
Flowers	-	-	6 (1)	6 (1)
Seeds	1 (0)	-	9 (2)	10 (2)
Fruits	10 (0)	3 (3)	14 (5)	27 (8)
Mature leaves	16 (4)	3 (3)	-	19 (7)
Fallen seeds	-	1 (1)	-	1 (1)
Total	28 (5)	7 (7)	34 (9)	69 (21)

Table 1.2

Correlation between availability of each food category and temperature

Food category	R	
Young leaves	-0.09	ns
Flowers	-0.78	$p < 0.01$
Seeds	0.48	ns
Fruits	-0.76	$p < 0.05$
Mature leaves	0.63	ns
Fallen seeds	-0.35	ns

Table 1.3

Correlation between feeding on each food category

	R					
	Flowers	Seeds	Fruits	M.leaves	F.seeds	Insects
Young leaves	0.06	-0.36	-0.45	0.76 *	-0.31	-0.15
Flowers		-0.37	-0.44	0.30	0.12	-0.48
Seeds			0.32	-0.66 *	-0.47	0.67 *
Fruits				-0.72 *	-0.41	0.42
Mature leaves					0.16	-0.59 +
Fallen seeds						-0.59 +

+: $p < 0.1$, *: $p < 0.05$

Table 1.4

Regression coefficients between feeding on each food category and availability, and temperature

Food category	Availability	Temperature
Young leaves	0.75 *	-0.06
Flowers	0.62 +	-0.31
Seeds	0.86 **	0.76 *
Fruits	-0.35	0.47
Mature leaves	-0.20	-0.56 +
Fallen seeds	0.35	-0.82 **
Insects	-	0.92 ***

+ $p < 0.1$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

Table 2.1

Hours spent in each activity (upper half) and percent of time spent in each activity (lower half) per half-month (n=22)

	Day length	Feed	Move	Active behavior	Social groom	Inactive	Total inactive	Other
Mean ± SD (hour)	12.33±1.40	3.97±1.06	2.85±0.78	6.82±0.94	2.31±0.63	2.85±1.18	14.52±0.90	0.35±0.24
Range (hour)	10.11-14.21	2.65-5.67	1.75-4.60	5.26-8.72	0.61-3.49	0.86-4.85	12.49-16.33	1.10-0.09
CV	0.11	0.27	0.27	0.14	0.27	0.42	0.06	0.69
Mean ± SD (%)	—	32.7±9.8	23.0±5.1	55.7 ±8.1	18.9±5.9	22.6 ±7.8	—	2.8 ±1.7
Range (%)	—	19.0-53.4	15.5-34.5	45.8-77.7	6.0-30.1	7.9-34.1	—	0.9-7.8

Table 2.2

Time spent feeding on each food category per half-month (n=22)

	Fruits	Seeds	Insects	Fungi	Mature leaves	Young leaves	Flowers	Fallen seeds	other
Mean±SD (%)	33.4±25.1	10.4±15.4	8.5±7.3	2.0±2.3	19.5±19.0	3.6±6.8	5.5±9.7	11.8±15.7	5.3±3.3
Range (%)	1.2-84.0	0.0-53.6	0.7-25.0	0.0-8.3	0.3-61.9	0.0-31.8	0.0-36.7	0.4-59.6	1.9-15.8

Table 2.3

Mean crown areas of food trees, density of potential food trees, and number of available months of each food

Species	Part	MCAFT(m^2)	n	TSF (%) mean	TSF (%) max	Density (No/ha)	SA (ha)	Available month
Rhus succedanea	Se	25.3	19	3.3	41.6	5.7	2.45	6
Lithocarpus edulis	Se	34.4	5	0.9	13.5	4.1	2.45	4
Euscaphis japonica	Se	8.2	8	0.7	11.2	1.6	2.45	2
Distylium racemosum	Se	36.8	17	3.1	38.0	1.2	2.45	5
Castanopsis sieboldii	Se	17.4	6	0.4	8.2	0.8	2.45	1
Myrica rubra	Fr	21.2	70	8.5	73.5	11.0	2.45	3
Symplocos glauca	Fr	7.3	6	0.9	17.9	5.7	2.45	4
Neolitsea sericea	Fr	26.6	7	0.8	12.1	4.5	2.45	10
Ficus erecta	Fr	33.0	20	2.3	10.3	3.7	2.45	12
Machilus thunbergii	Fr	36.7	28	2.9	22.5	3.7	2.45	2
Litsea acuminata	Fr	31.6	7	1.0	8.7	2.9	2.45	5
Swida macrophylla	Fr	24.9	12	0.9	11.6	1.6	2.45	2
Trema orientalis	Fr	49.7	4	0.5	4.0	1.6	2.45	10
Oreocnide pedunculata	Fr	16.0	5	0.6	4.9	1.2	2.45	10
F. superba japonica	Fr	120.2	14	7.1	41.3	0.3	ca. 30	12
O. pedunculata	Fl	12.5	14	3.2	36.3	6.5	2.45	2
Quercus salicina	Fl	41.0	5	0.2	1.9	3.7	2.45	2
F. erecta	Ml	17.6	8	1.1	7.0	15.9	2.45	12
Schefflera octophylla	Ml	22.1	5	0.8	6.7	9.8	2.45	12
O. pedunculata	Ml	10.3	16	1.6	5.8	7.8	2.45	12
Daphniphyllum teijsmannii	Ml	19.7	14	1.4	9.6	7.3	2.45	12
S. prunifolia	Ml	11.7	6	0.9	11.3	6.5	2.45	12
S. glauca	Ml	8.8	5	0.3	3.8	4.9	2.45	12
Callicarpa spp	Ml	3.0	8	1.5	6.1	1.6	2.45	10
T. orientalis	Ml	35.4	19	4.1	17.7	1.6	2.45	12
Eurya emarginata	Ml	7.5	5	0.6	5.2	0.8	2.45	12
F. superba japonica	Ml	121.2	11	0.8	5.4	0.3	ca. 30	12
Morus australis	Yl	39.5	13	1.3	7.0	0.0	2.45	12

Part: eaten part of the species; Fr, fruit; Fl, flower; Se, seed;
Ml, mature leaf; Yl, young leaf.

MCAFT: mean crown area of the food trees

TSF: mean and maximum time spent feeding on the item in the 22 half-months

Density: density of the trees that had equal to or larger crown area than MCAFT

SA: surveyed area for the food species

Available month: number of available months of the food in a year

Table 4.1

FOOD CATEGORIES EATEN IN EACH HALF-MONTH

PERIOD		HALF-MONTH	N	FOOD CATEGORY (% FEEDING TIME) FRUIT	FLOWER	LEAF	FALLEN SEED	INSECT	OTHER
Period 1	1990	Feb 6-21 (LFEB1)	1669	3.5	7.1	30.2	52.1	3.1	4.0
Non-fruit-eating season (Non-FES)		Mar 1-15 (EMAR)	755	12.1	36.7	22.5	23.7	0.9	4.1
		May 1-15 (EMAY)	760	40.3	2.2	38.3	0.9	7.0	11.3
		Dec 16-31 (LDEC)	440	22.3	0.0	33.4	34.1	2.0	8.2
	1991	Feb 22- Mar 7 (LFEB2)	795	5.9	20.4	55.7	2.9	1.6	13.5
Period 1	1990	May 16-30 (LMAY)	524	84.7	0.0	3.2	0.6	6.3	5.2
Fruit-eating season (FES)		Jun 1-15 (EJUN)	332	73.8	0.0	1.2	0.9	16.3	7.8
		Jun 16-30 (LJUN)	662	57.9	0.0	1.4	0.2	22.7	18.0
		Aug 12-27 (LAUG)	459	61.4	0.0	0.7	0.4	23.3	14.2
Period 2	1992	Jan 20- Feb 3 (LJAN)	140	28.6	5.0	48.6	8.6	6.4	2.9
Non-fruit-eating season (Non-FES)		Apr 16-30 (LAPR)	242	8.3	2.9	73.1	0.0	9.9	5.8
Period 2	1991	Sep 15-30 (LSEP)	223	83.4	0.0	3.1	0.9	5.8	6.7
Fruit-eating season (FES)		Nov 1-15 (ENOV)	118	75.4	4.2	3.4	5.1	3.4	8.5
		Dec 1-15 (EDEC)	169	83.4	1.8	6.5	1.2	3.6	3.6

Table 4.2

ACTIVITY BUDGET IN EACH HALF-MONTH

PERIOD	HALF-MONTH	NO. SCAN	ACTIVITY (% OBSERVATION TIME) FEED	MOVE	GROOM	SELF-GROOM	REST	OTHER	ACTIVE BEHAV. *1	CV *2	P OF K-S test *3
Period 1	LFEB1	332	50.1	18.0	21.7	1.4	8.1	0.7	68.1	0.48	<.001
Non-FES	EMAR	184	38.8	17.0	26.4	1.3	16.0	0.6	55.8	0.56	.077 ns
	EMAY	206	35.9	20.8	19.5	1.0	22.3	0.7	56.6	0.56	.031
	LDEC	74	53.1	21.1	8.0	1.8	15.7	0.2	74.3	0.37	.017
	LFEB2	266	32.9	15.4	30.0	2.7	19.0	0.0	48.3	0.65	.045
Period 1	LMAY	145	38.1	24.6	17.4	1.3	17.2	1.2	61.0	0.48	.110 ns
FES	EJUN	178	19.1	26.8	14.6	1.4	31.9	6.2	44.5	0.65	.039
	LJUN	337	19.6	27.3	12.5	0.5	35.0	5.3	46.9	0.64	.012
	LAUG	244	19.9	28.7	21.0	2.4	26.8	1.2	48.6	0.66	.047
Period 2	LJAN	105	27.5	20.6	27.1	4.8	19.7	0.2	48.1	0.75	.028
Non-FES	LAPR	144	38.1	18.8	8.8	0.6	33.8	0.0	56.9	0.62	.004
Period 2	LSEP	151	26.4	22.5	21.1	2.6	26.7	0.6	49.0	0.77	.001
FES	ENOV	114	23.1	27.0	19.6	0.7	29.5	0.0	50.1	0.73	.003
	EDEC	123	28.9	23.9	24.6	1.6	20.7	0.3	52.8	0.71	.010

*1: Active behav. = moving and feeding.

*2: Coefficient of variation of % of monkeys in each scan engaged in active behaviors.

*3: Probability from Kolmogorov-Smirnov normality test.

Table 4.3

LARGEST DISTANCE BETWEEN VISIBLE MONKEYS AND NUMBER OF FOOD ITEMS IN EACH SCAN

		ACTIVE PHASE		NON-ACTIVE PHASE			
PERIOD	HALF-MONTH	N	LD (m)	N	LD (m)	N	NO. FOOD ITEMS
Period 1	LFEB1	-	-	-	-	191	1.72
(Non-FES)	FMAR	-	-	-	-	94	2.05
	FMAY	-	-	-	-	109	1.82
	LDEC	17	25.9	15	21.0	48	2.06
	LFEB2	-	-	-	-	131	2.43
Period 1	LMAY	-	-	-	-	82	1.09
(FES)	FJUN	-	-	-	-	81	0.74
	LJUN	-	-	-	-	164	0.64
	LAUG	56	23.9	67	22.8	129	0.67
Period 2	LJAN	54	14.4	50	9.4	54	1.46
(Non-FES)	LAPR	81	14.0	62	11.8	82	1.45
Period 2	LSEP	74	17 1	75	13.6	75	0.93
(FES)	ENOV	54	13.9	60	9.8	54	0.94
	EDEC	62	15.6	60	7.7	62	1.27

Non-FES: Non-fruit-eating season, FES: Fruit-eating season

Table 4.4

PROPORTION OF EACH PHASE THAT WAS 40 MINUTES OR LONGER

PERIOD	HALF-MONTH	ACTIVE PHASE No.SCAN	%	NON-ACTIVE PHASE No.SCAN	%
Period 1 (Non-FES)	LFEB1	168	78.6	136	72.1
	FMAR	77	72.7	88	68.2
	FMAY	102	78.4	83	78.3
	LDEC	40	100.0	20	60.0
	LFEB2	123	86.2	124	89.5
Period 1 (FES)	LMAY	68	51.5	59	47.5
	FJUN	70	42.9	92	72.8
	LJUN	135	50.4	165	70.9
	LAUG	97	76.3	108	81.5
Period 2 (Non-FES)	LJAN	47	73.4	48	61.7
	LAPR	79	76.6	60	79.2
Period 2 (FES)	LSEP	71	68.0	73	73.3
	ENOV	45	33.3	52	46.2
	EDEC	50	63.4	60	75.3

Non-FES: Non-fruit-eating season, FES: Fruit-eating season

Table 4.5

PROPORTION OF FEEDING TIME SPENT ON EACH FOOD CATEGORY

HALF-MONTH			PHASE	N	FRUIT (%)	FLOWER (%)	LEAF (%)	FALLEN SEED (%)	INSECT (%)	OTHER (%)
Period 1 (Non-FES)	LFEB1	**	A	1088	2.9	7.1	30.2	53.6	2.7	3.5
			N	350	6.0	7.7	31.1	46.0	4.3	4.9
	FMAR	**	A	434	6.5	39.2	28.1	24.0	0.2	2.1
			N	182	18.7	41.2	13.2	19.8	2.2	4.9
	FMAY	NS	A	485	44.3	1.6	41.0	0.2	4.5	8.2
			N	153	47.7	4.6	19.6	2.0	11.1	15.0
	LDEC	**	A	279	15.4	0.0	36.9	40.5	2.9	4.3
			N	48	52.1	0.0	35.4	8.3	0.0	4.2
	LFEB2	NS	A	541	6.1	19.0	57.1	3.0	1.8	12.9
			N	192	4.2	25.2	51.0	2.6	1.0	15.6
Period 1 (FES)	LMAY	**	A	316	88.6	0.0	0.6	0.6	5.4	4.7
			N	118	75.4	0.0	3.4	1.7	11.1	8.5
	FJUN	**	A	222	78.8	0.0	0.0	0.9	14.9	5.4
			N	67	59.7	0.0	6.0	1.5	19.4	13.4
	LJUN	NS	A	412	57.3	0.0	1.9	0.0	22.3	18.4
			N	151	59.6	0.0	0.0	0.0	21.2	19.2
	LAUG	**	A	273	67.4	0.0	0.4	0.4	21.2	10.6
			N	67	46.3	0.0	1.5	1.5	38.8	11.9
Period 2 (Non-FES)	LJAN	NS1	A	99	25.3	6.1	56.6	8.1	2.0	2.0
			N	19	31.6	5.3	10.5	10.5	31.6	10.5
	LAPR	NS1	A	204	9.3	3.4	75.5	0.0	8.3	3.4
			N	30	3.3	0.0	56.7	0.0	20.0	2.0
Period 2 (FES)	LSEP	**	A	184	87.5	0.0	2.2	0.5	3.3	6.5
			N	23	43.5	0.0	13.4	4.3	30.4	8.7
	ENOV	**1	A	76	81.6	2.6	3.9	1.3	2.6	7.9
			N	14	42.9	0.0	7.1	21.4	7.1	21.4
	EDEC	NS	A	110	80.9	2.7	10.0	0.9	1.8	3.7
			N	27	81.5	0.0	0.0	3.7	11.1	3.6

A: active phase, N: non-active phase.

Difference of % of fruits and non-fruit foods between the phases was tested.

Chi-square test, **: $p < 0.01$, NS: $p > 0.05$

Fisher's exact probability test, **1: $p < 0.01$, NS1: $p > 0.05$

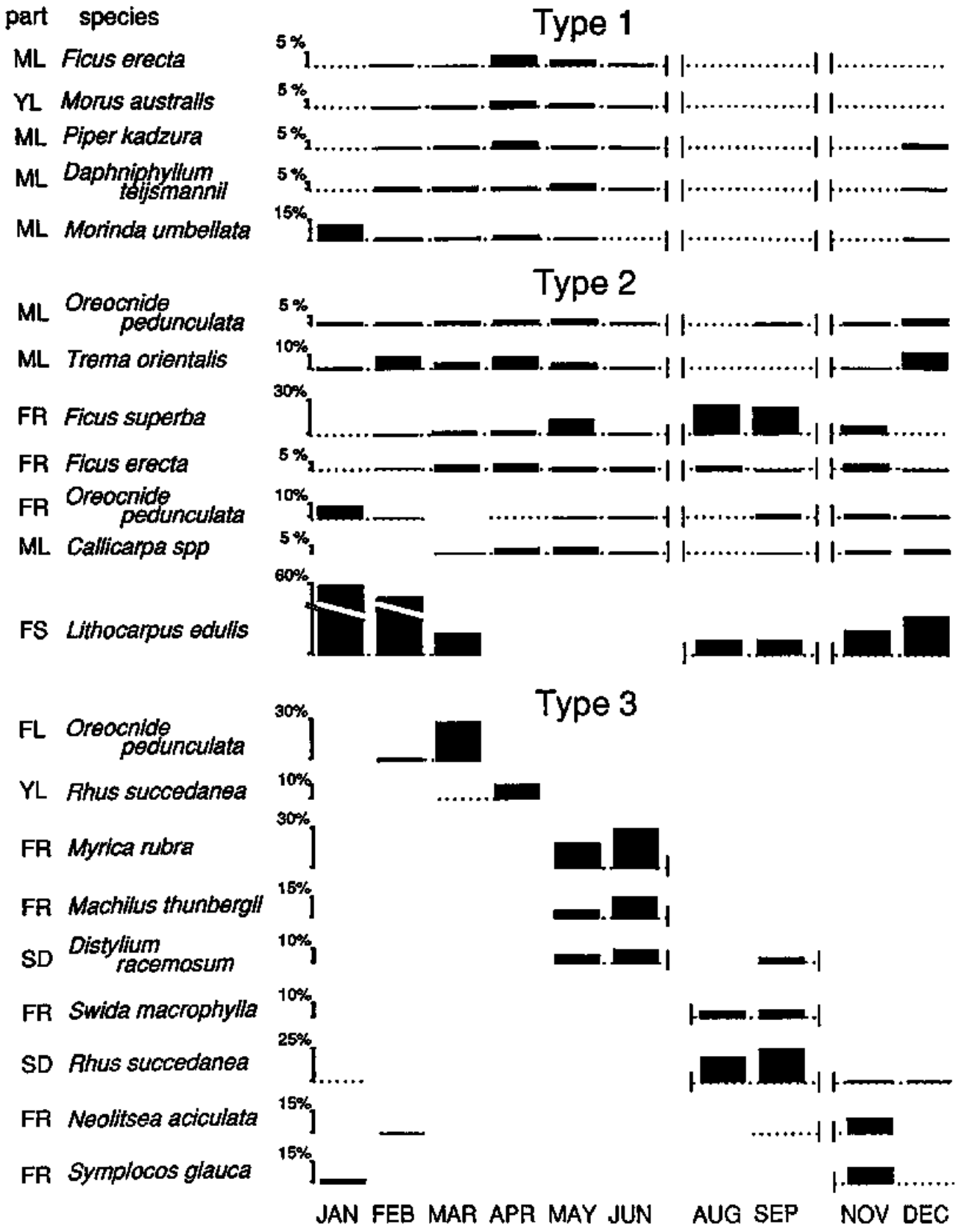

Figure 1 1
Period of availability and time spent feeding on main plant food items. Dotted line shows available periods of the items. Solid bars show time spent feeding on the items. ML. mature leaves, YL. young leaves, FS: fallen seeds, FL. flowers, FR: fruits, SD: seeds.

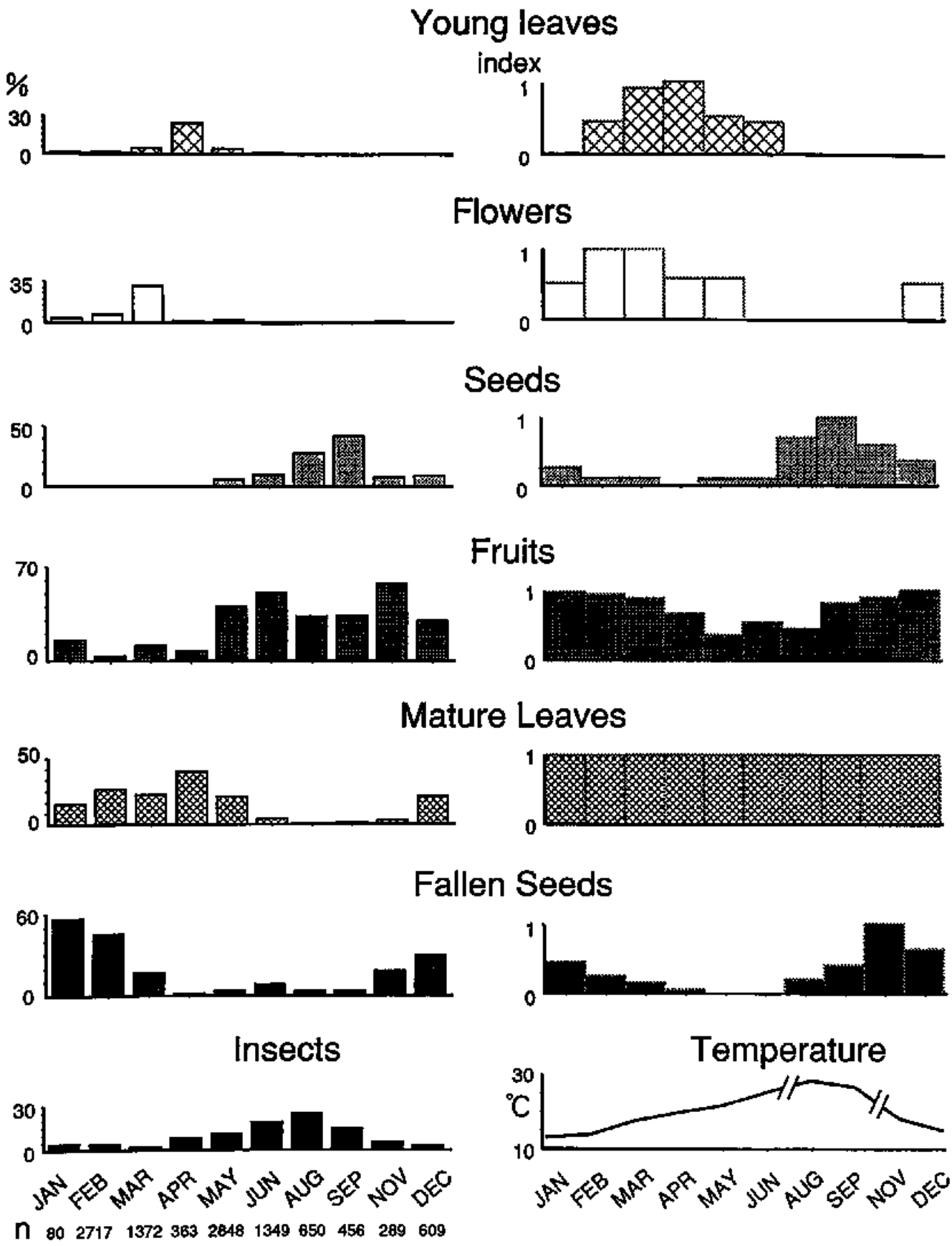

Figure 1.2
Time spent feeding on each food category (left), availabilies of each plant food category (above right) and monthly temperatures (bottom right).

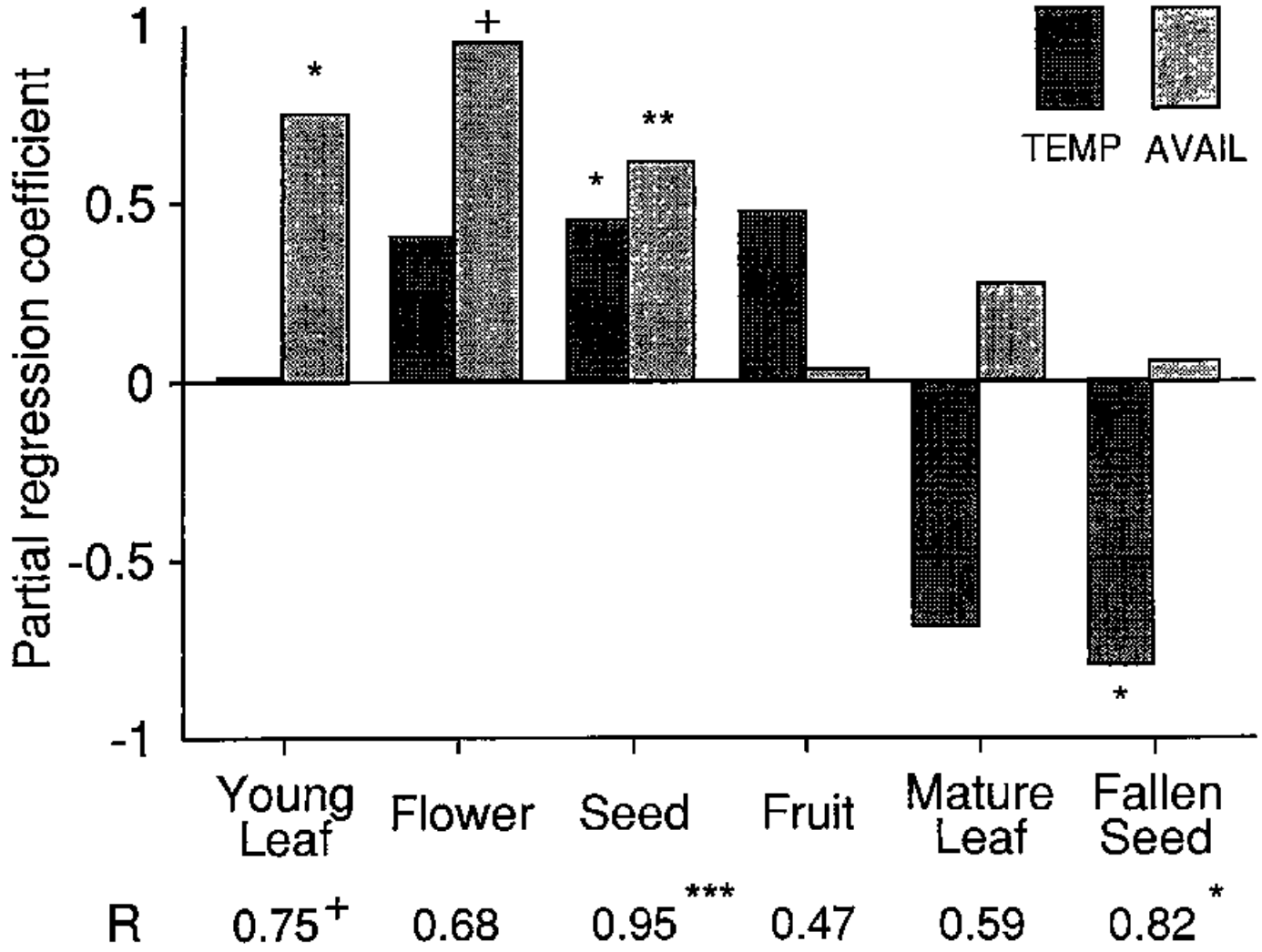

Figure 1.3

Partial regression coefficients of temperature and avilability from multiple regression analysis. Figures at the bottom show coefficients of multiple regression. +: $p < 0.1$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

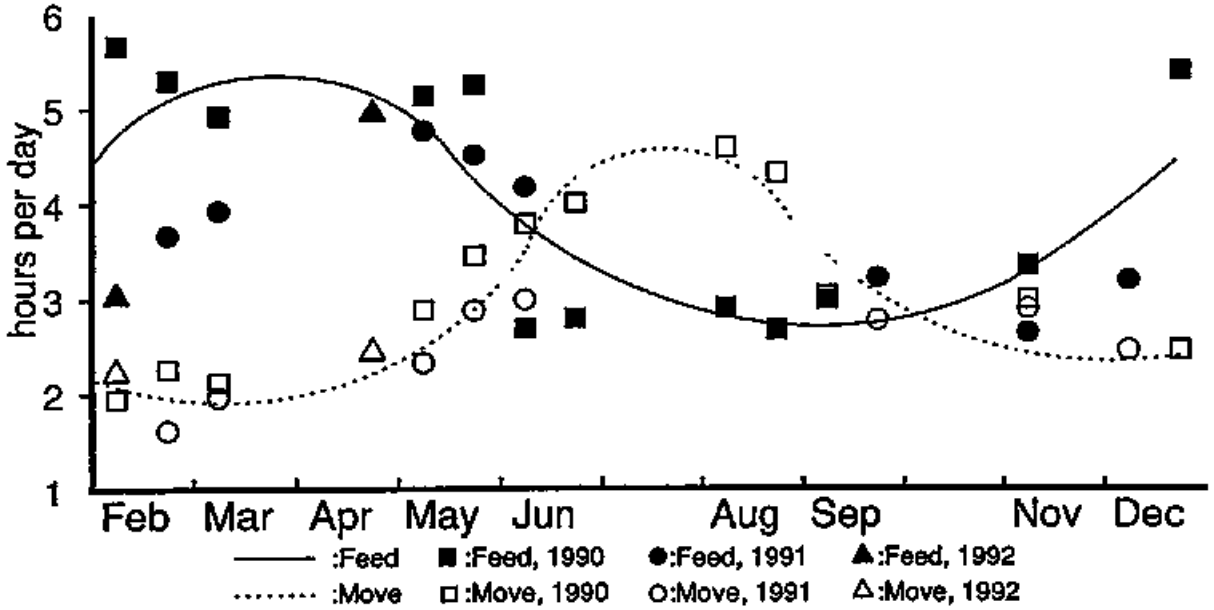

Figure 2.1

Time spent feeding and moving in each half-month (hours per day). Solid and dotted lines were drawn by hand.

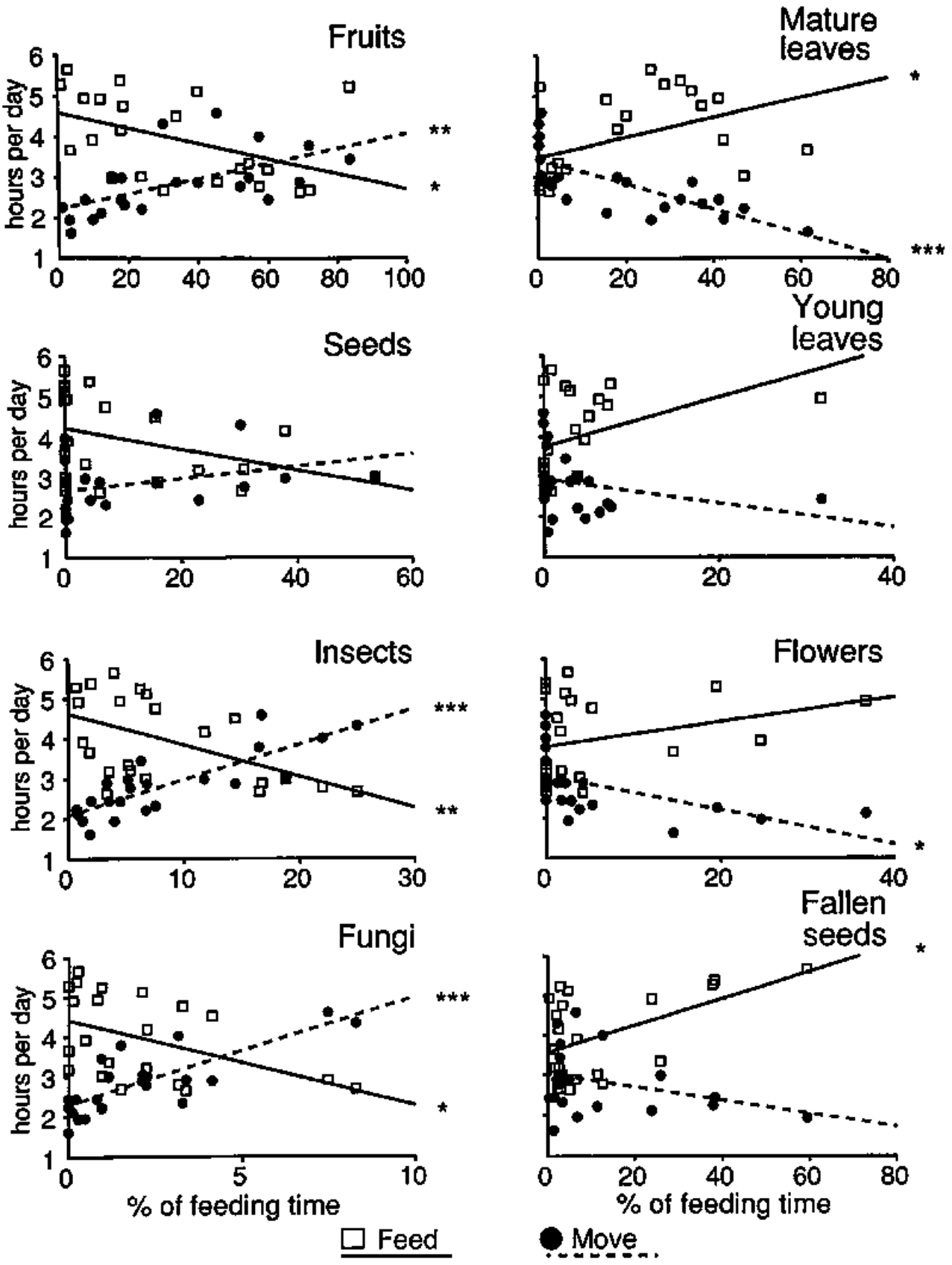

Figure 2.2
Correlations, across half-months, between percentages of total feeding time spent feeding on each food category and each of feeding time and moving time (hours per day). Squares show time spent feeding, and circles show time spent moving in each half-month. Solid and broken lines indicate regression curves of feeding on each food and feeding time, and moving time, respectively. Significance levels of correlation coefficients are shown by * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$.

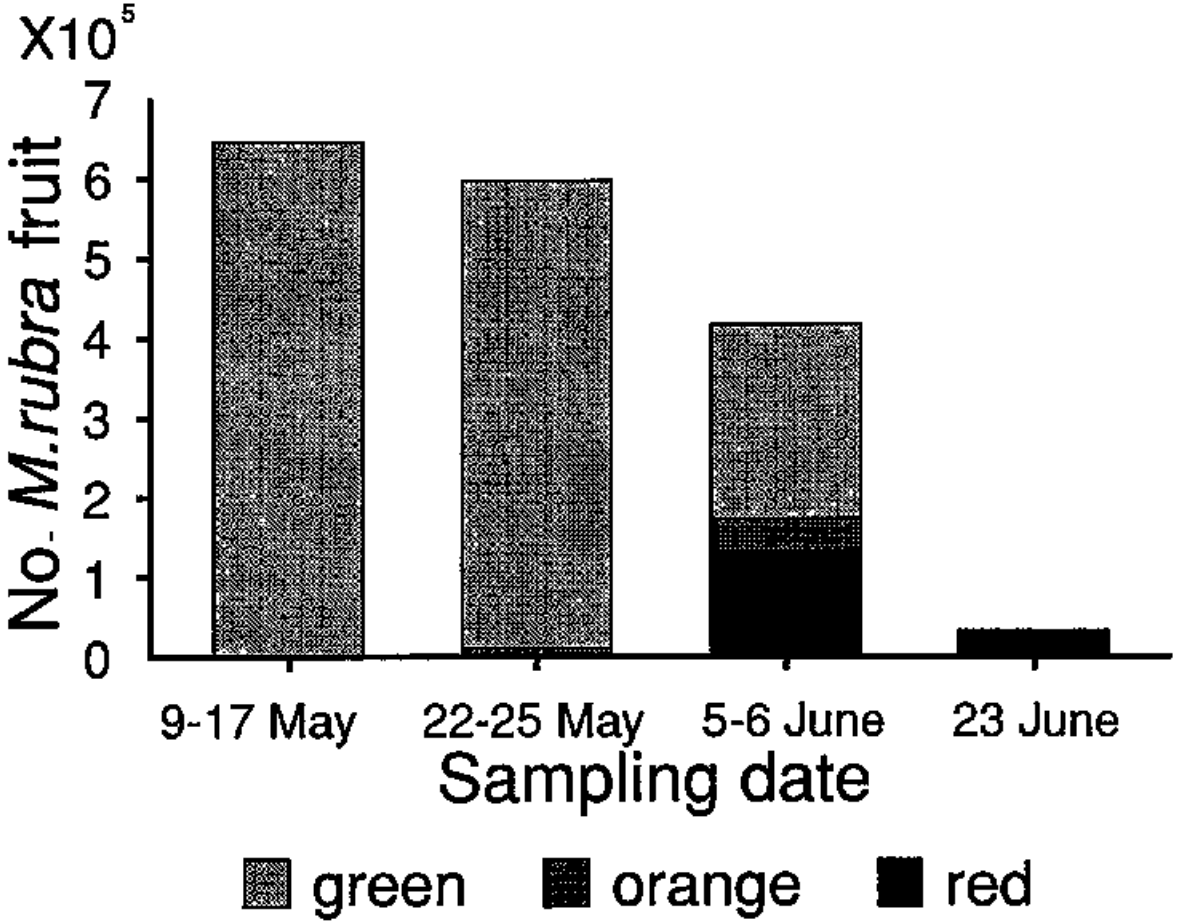

Figure 3.1

Changes in the number of unripe, semi-ripe and ripe *Myrica rubra* fruit on 7 sample trees. The fruit decreased rapidly after the second sampling.

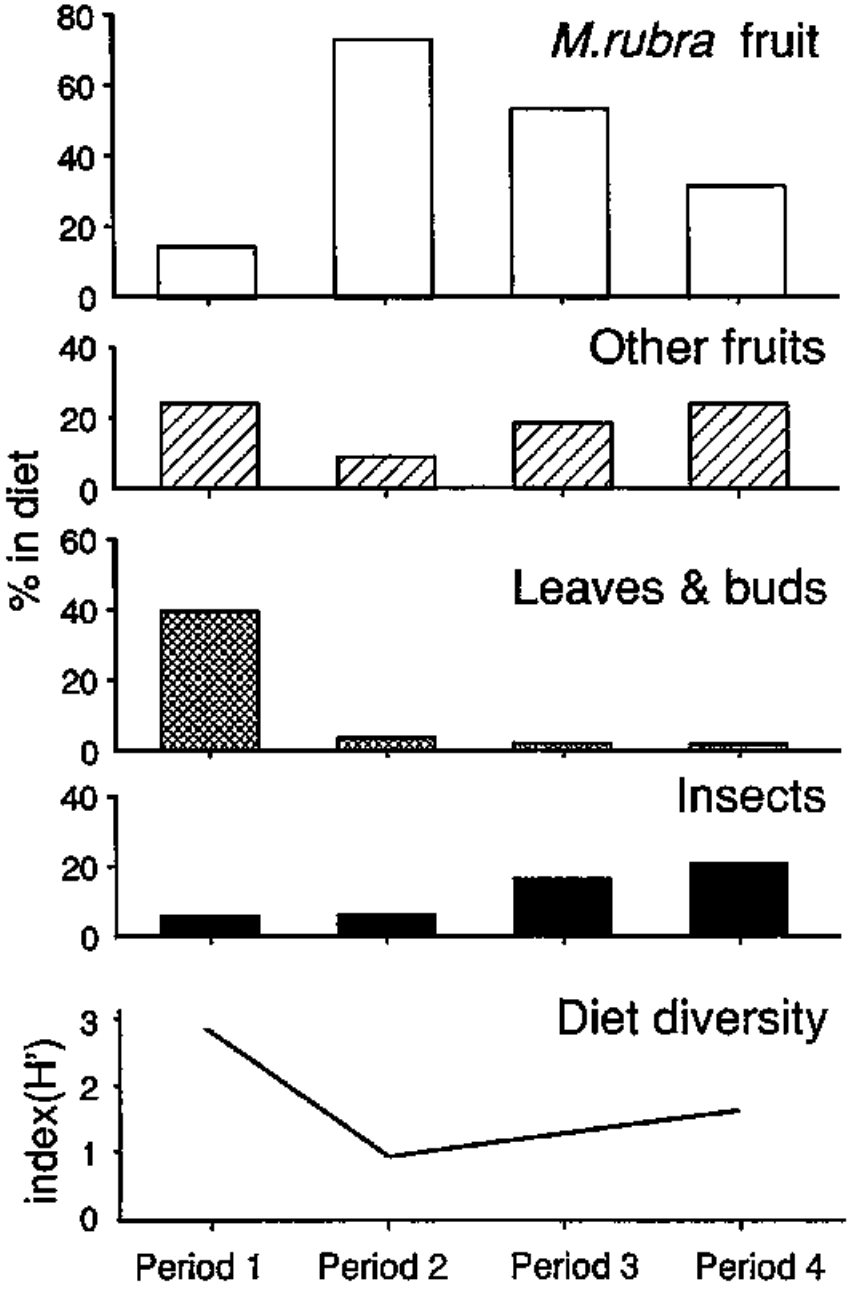

Figure 3.2

Percentages of four categories of food items in the diet (upper) and dietary diversity (lower) in each period. Diversity was expressed by the index of Shannon's formula (Pielou, 1966).

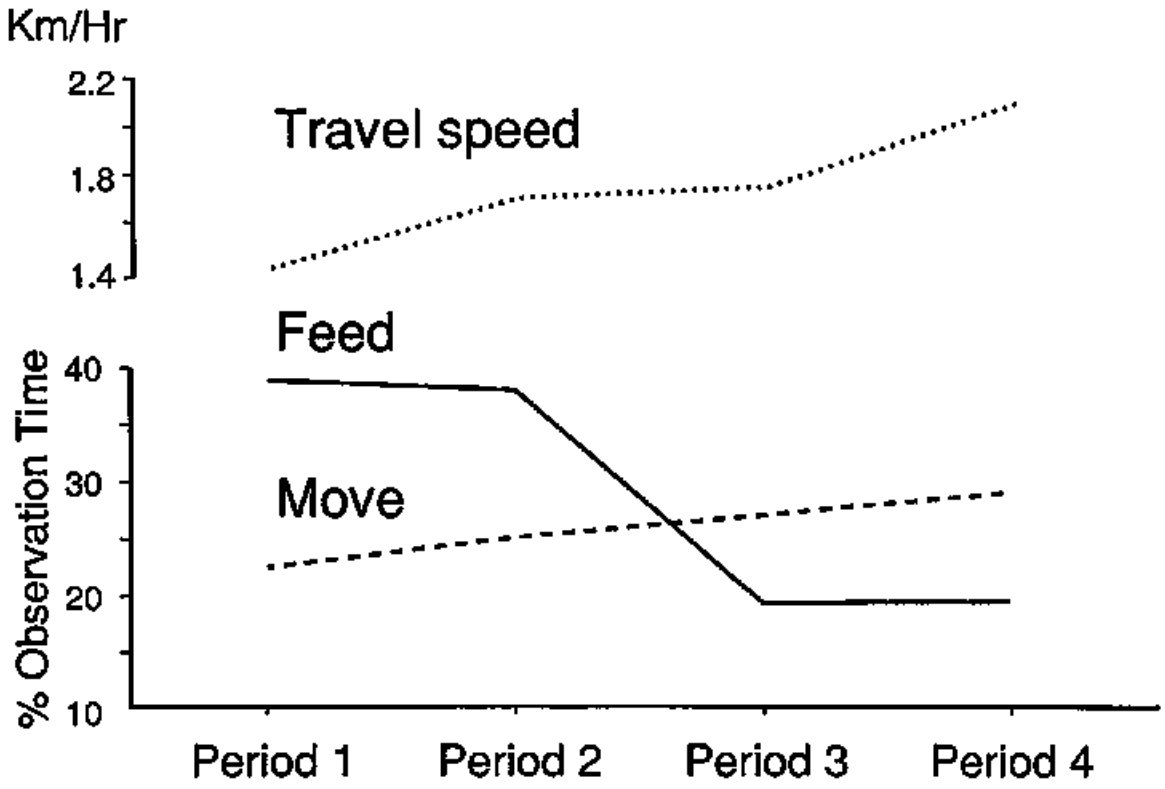

Figure 3.3

Mean travel speed (upper) and time spent feeding and moving (lower) in each period.

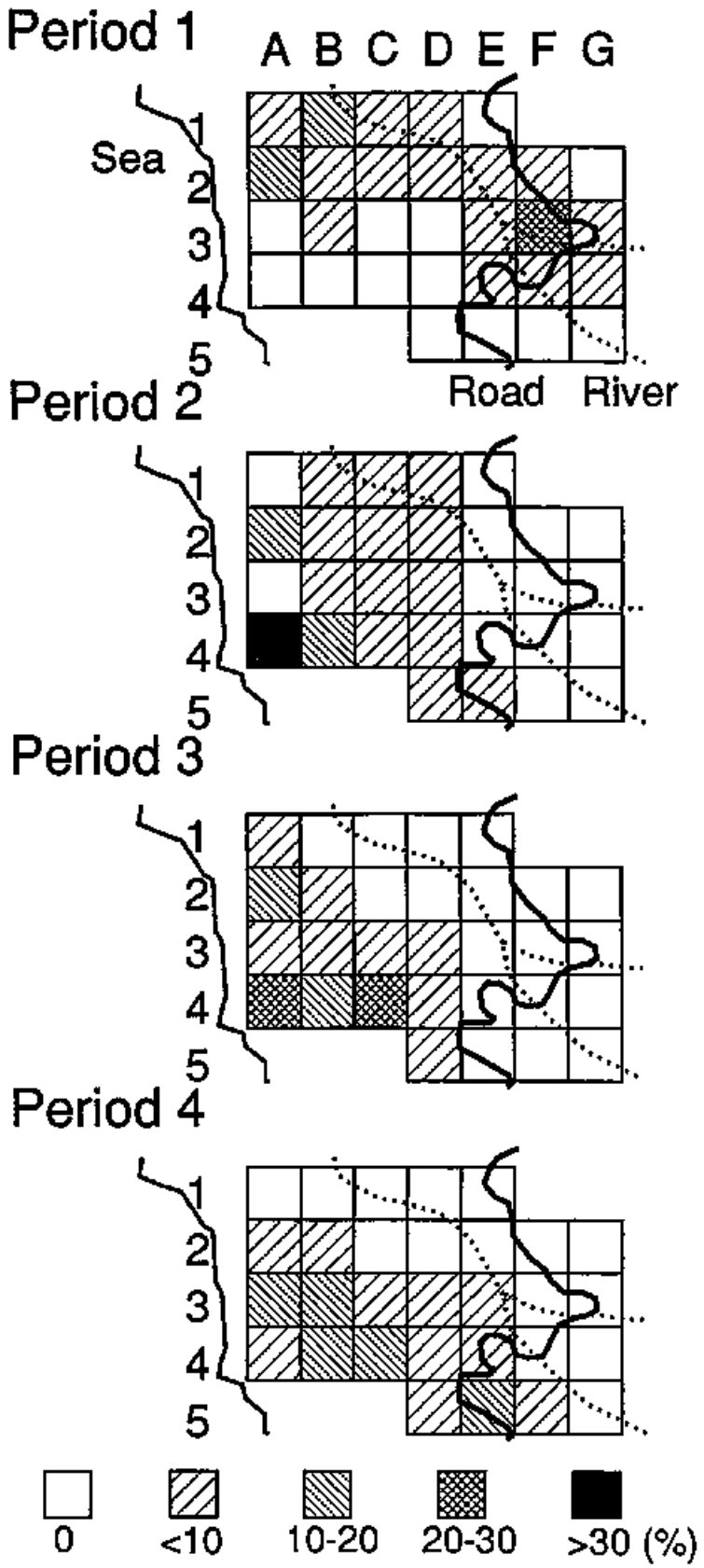

Figure 3.4

Range-use by the study group in each period. The study area was covered by warm-temperate broad-leaved forest. A road ran through from north to south (thick line), and streams from southeast to northwest (dotted lines).

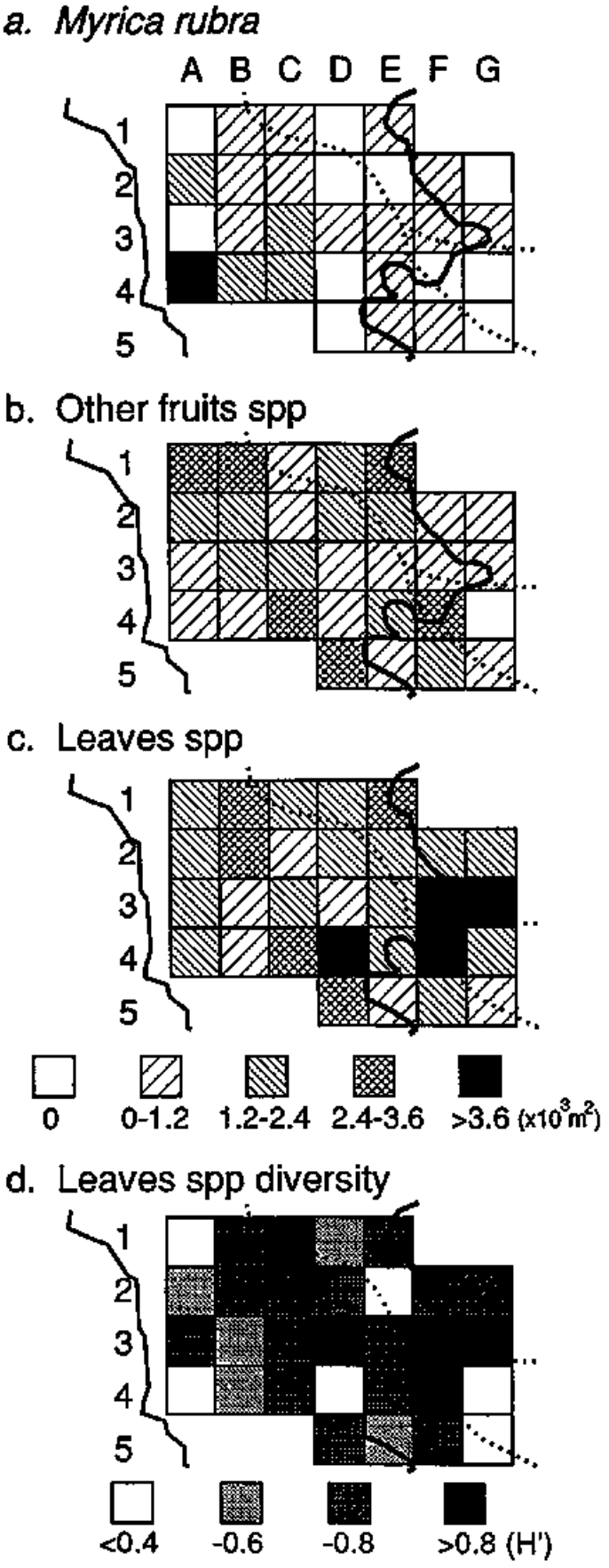

Figure 3.5

Vegetation of 30 quadrats (100m X 100m) were surveyed in study area. a: Crown densities of *Myrica rubra,* b: top 2 other fruit species, c: top 5 leaf-food species, d: diversity of leaf-food species in each quadrat (total 19 spp).

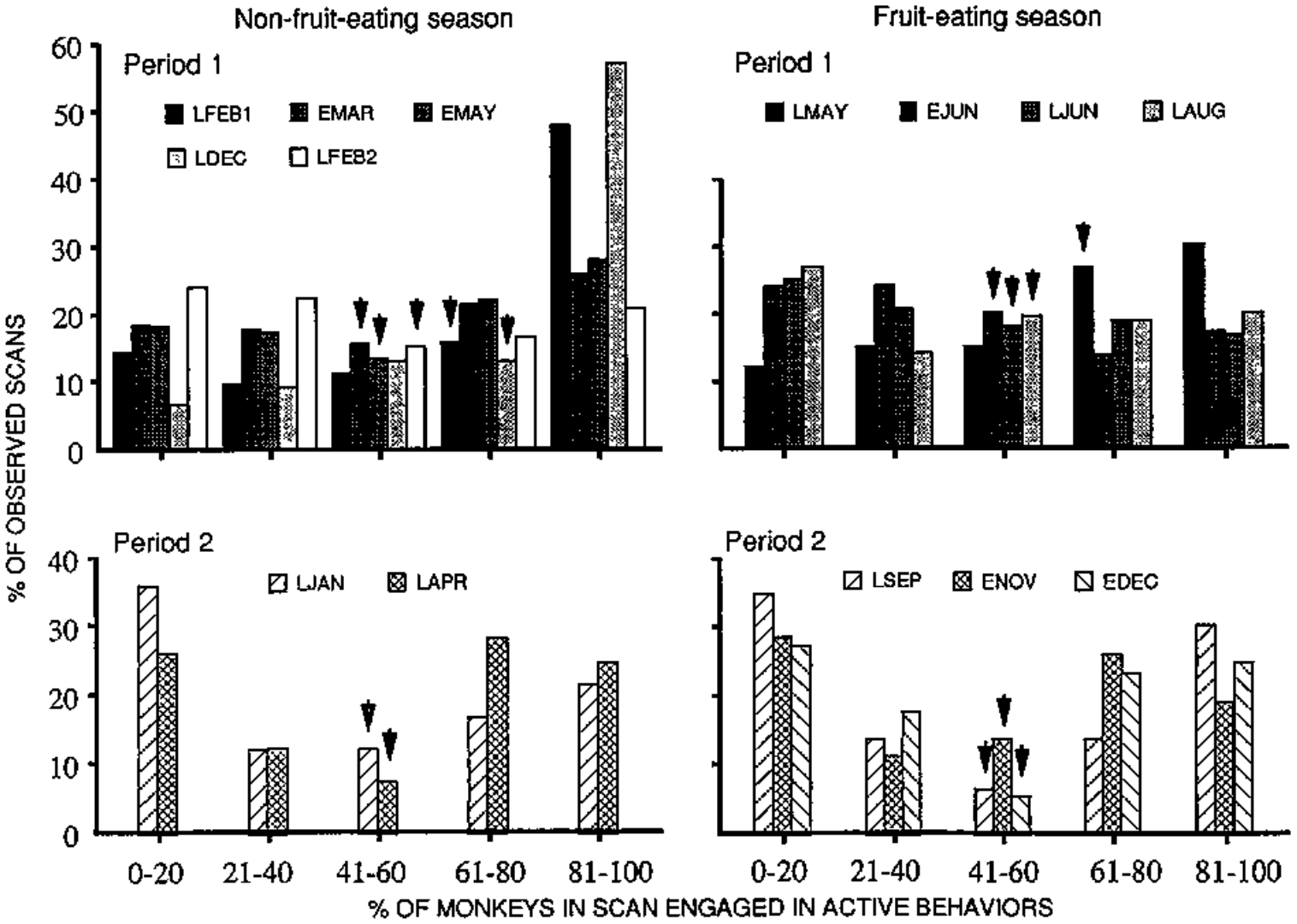

Figure 4.1
Percentage of all scans in which different percentage of monkeys observed were engaged in active behaviors. If the monkeys behaved randomly, the shape of the histogram would show a normal distribution with the value of active behaviors in Table 4.2 as a mean shown by arrows.

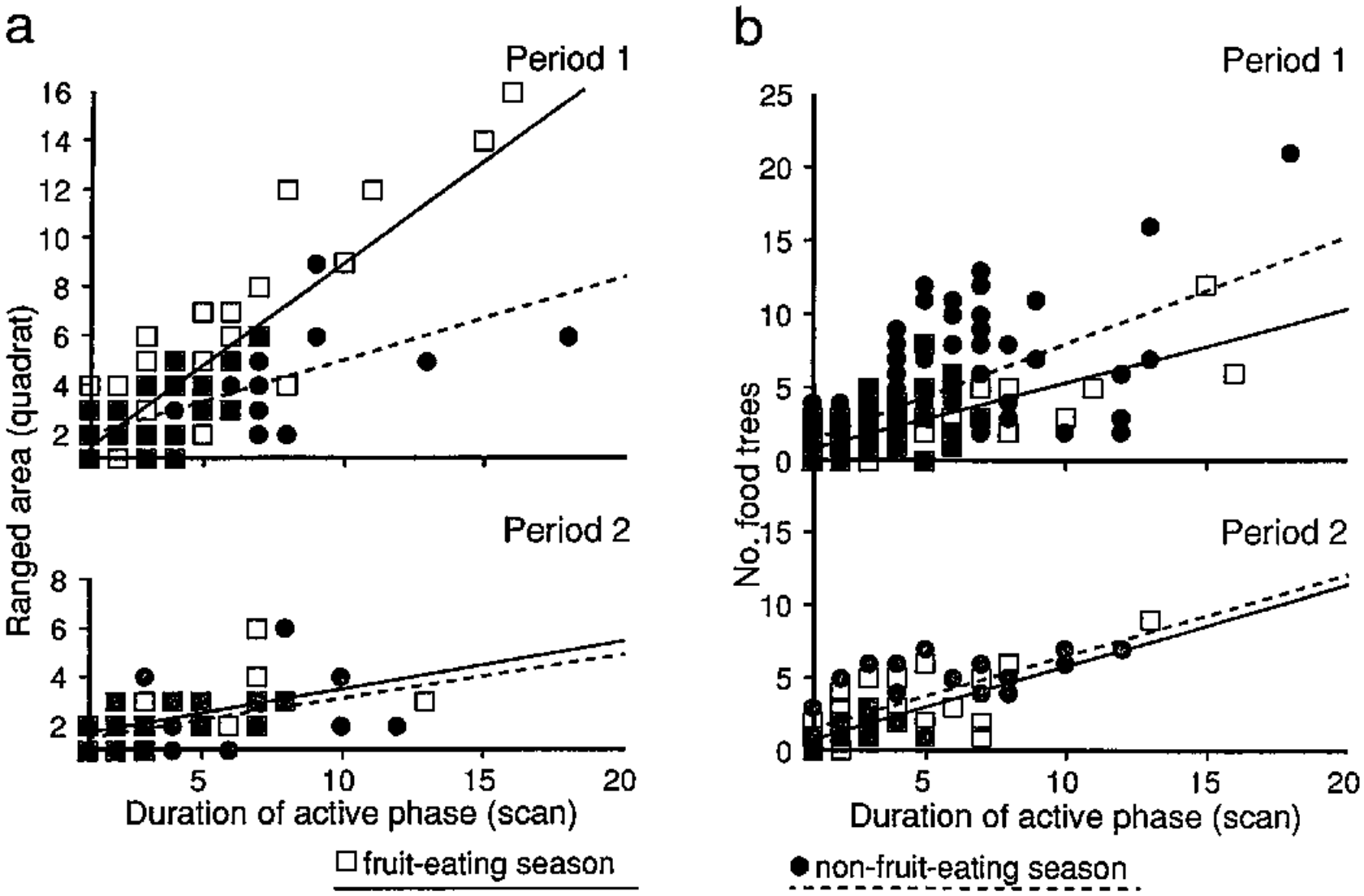

Figure 4.2

Relation between duration of the active phase and range area(a), and number of food trees (b) during that phase. Open squares: active phase in fruit-eating season. Solid circles: active phase in non-fruit-eating season. Solid lines: regression lines of fruit-eating season. Dotted lines: non-fruit eating season.